FEEDING ECOLOGY OF LARVAL AND JUVENILE WALLEYE POLLOCK (*THERAGRA CHALCOGRAMMA*) AND PACIFIC COD (*GADUS MACROCEPHALUS*) IN THE SOUTHEASTERN BERING SEA

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A

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Abstract:

Poor recruitment success during warm years (e.g., 2001-2005) was hypothesized to lead to reduced gadid recruitment in the southeastern Bering Sea. These groundfishes are of particular importance, both commercially and ecologically in the southeastern Bering Sea. The spatial and temporal overlap of early life stages of walleye pollock and Pacific cod may explain their strongly correlated recruitment trends in the southeastern Bering Sea. The goal of this study was to compare feeding patterns of larval and juvenile walleye pollock (*Theragra chalcogramma*) and Pacific cod (*Gadus macrocephalus*) in the southeastern Bering Sea, and to assess the possibility of prey resource competition. Larvae and juveniles from both species collected between May and September 2008, an exceptionally cold year, were used to analyze stomach contents. Fish body size was most consistently related to diet composition within species, however, spatial and depth factors also had an influence. Feeding success and diet composition of these two gadid species were consistently different throughout the spring, summer, and especially fall seasons. Pacific cod larvae and juveniles consistently consumed larger prey items in every season and progressively fewer prey items, especially in the fall. This data suggests that competition for prey resources was unlikely during cold 2008.

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GENERAL INTRODUCTION

In the southeastern Bering Sea, walleye pollock and Pacific cod exhibit similarities in life history patterns and spatial distribution in their early life stages. Both species spawn from January to April (Bacheler et al. 2010, Shimada & Kimura 1994) in relatively deep waters over the continental shelf, along the Alaska Peninsula, and near the Pribilof Islands (Fritz et al. 1993, Bacheler et al. 2010). As a result of this temporal and spatial overlap of early pelagic life stages and because of similarities in body size and shape, it is reasonable to assume that walleye pollock and Pacific cod may exploit similar prey fields, resulting in a potential for dietary overlap and the possibility for competition if prey resource are limited.

Determining feeding success and dietary overlap will allow us to compare and quantify patterns of resource allocation and the probability of feeding competition between early life stages of walleye pollock and Pacific cod. Seasonal sampling for this study was conducted in 2008, an exceptionally cold year characterized by heavy ice cover, late ice retreat, and cold temperatures. These conditions may have affected the abundance and composition of available prey for larval and juvenile walleye pollock and Pacific cod (Coyle et al. 2008 & 2011, Hunt et al. 2011). The overall goal of this study was therefore to examine feeding success and dietary patterns of walleye pollock and Pacific cod during cold conditions in the southeastern Bering Sea and to assess the potential for dietary competition between larval and juvenile stages of two commercially important groundfish species.

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INTRODUCTION

Walleye pollock (*Theragra chalcogramma*) and Pacific cod (*Gadus macrocephalus*) are two of the most commercially important groundfish species in the Bering Sea, with an annual harvest ranging from 0.48-1.40 million metric tons (Ianelli et al. 2011) for walleye pollock in the southeastern Bering Sea and 120,000-183,000 metric tons for Pacific cod in the eastern Bering Sea over the past decade (Thompson et al. 2011). In addition, these species are of ecological importance within the southeastern Bering Sea ecosystem (Aydin & Mueter 2007), as they serve as prey for seabirds (Decker & Hunt 1996), marine mammals (Sinclair et al. 1994), and piscivorous fishes, including older age-classes of walleye pollock (Bailey 1989). Both species are also important predators, with walleye pollock exerting predation pressure on other pelagic forage fishes, such as Pacific sand lance (*Ammodytes hexapterus*) and capelin (*Mallotus villosus*) (Coyle et al. 2011), while Pacific cod are known to incorporate large amounts of commercially important crab species in their diet (Livingston 1989), such as red king crab (*Paralithodes camtschatica)* and both tanner and snow crab (*Chionoecetes bairdi* and *opilio)*. Thus, walleye pollock and Pacific cod play a central role in the food web of the southeastern Bering Sea. A better understanding of the ecology of these two species would advance our knowledge of ecosystem function in the southeastern Bering Sea.

During the most recent warm stanza (2001-2005), stock assessment of walleye pollock in the southeastern Bering Sea indicated a decline in biomass (Ianelli et al. 2011) that was hypothesized to be the result of poor recruitment success of the 2001-2005 cohorts. In contrast, recruitment for walleye pollock has been on the rise during the recent cold years, with strong cohorts in 2006 and 2008 (Ianelli et al. 2011). Similarly, the 2011 stock assessment for Pacific cod in the southeastern Bering Sea also indicated a rebounding population following recent lows in abundance in 2005 and biomass in 2007 (Thompson et al. 2011). Factors influencing these recruitment relationships are only partially understood, but recent research results suggest declining recruitment success of walleye pollock under predictions of climate warming (Mueter et al. 2011). These studies emphasize the importance of gaining a better understanding of conditions affecting the survival of larval and juvenile stages of these groundfishes, particularly during times of environmental transition.

In the southeastern Bering Sea, walleye pollock and Pacific cod exhibit similarities in life history patterns and spatial distribution in their early life stages. Both species spawn from January to April (Shimada & Kimura 1994, Bacheler et al. 2010) in relatively deep waters over the continental shelf, along the Alaska Peninsula, and near the Pribilof Islands (Fritz et al. 1993, Bacheler et al. 2010). Walleye pollock eggs tend to be slightly positively buoyant and pelagic, while Pacific cod eggs tend to be negatively buoyant and demersal (Dunn & Matarese 1987); however, post-hatch larvae from both species rise to the epipelagic layer to initiate feeding. Studies on Bering Sea ichthyoplankton assemblages show that gadids dominate the catch in the spring and summer (Matarese et al. 2003, Duffy-Anderson et al. 2006). Age-0 walleye pollock are ubiquitous and occur in varying numbers across the southeastern Bering Sea shelf; in contrast, Pacific cod are less abundant but share similar distributional patterns (Matarese et al. 2003, Duffy-Anderson et al. 2006). Specifically, both species have larval abundance maxima in the southeastern Bering Sea along the Alaska Peninsula and Aleutian Islands, particularly in and around Unimak Pass, as well as north of the Pribilof Islands (Matarese et al. 2003). During late spring and summer, pelagic larvae and juveniles are concentrated in the upper mixed layer (40-10 m). By the fall, juvenile walleye pollock disperse throughout the water column at standard lengths (SL) > 40 mm, while Pacific cod juveniles settle out to a demersal lifestyle earlier at > 35 mm SL (Blackburn & Jackson 1982, Nishiyama et al. 1986, Dunn & Matarese 1987, Rugen & Matarese 1988, Bailey 1989, Ciannelli et al. 1998). The spatial and temporal overlap of age-0 walleye pollock and Pacific cod may explain the strongly correlated trends in walleye pollock and Pacific cod recruitments in the southeastern Bering Sea (Mueter et al. 2009).

As a result of the spatial overlap of early pelagic life stages and because of similarities in body size and shape, it is reasonable to assume that walleye pollock and Pacific cod may exploit similar prey fields, resulting in a potential for dietary overlap and the possibility for competition if prey resource are limited. While numerous studies have been conducted on the diet of larval and juvenile walleye pollock, most of these diet studies focused either on larval fish in spring (Nishiyama et al. 1986, Hillgruber et al. 1995, Porter et al. 2005) or on juvenile stages later in the fall (Brodeur et al. 2000, Schabetsberger et al. 2000 & 2003, Coyle et al. 2008, Moss et al. 2009, Coyle et al.

2011). Substantially less is known about the feeding success and dietary patterns of age-0 Pacific cod (Abookire et al. 2007), particularly in the Bering Sea. However, knowledge about feeding patterns of early life stages of both species is of great importance in order to better understand factors impacting recruitment success, particularly in light of changing environmental conditions. Therefore, the goal of this study was to compare and contrast feeding patterns of age-0 walleye pollock and Pacific cod in the southeastern Bering Sea, incorporating samples from spring, summer, and fall of 2008.

Growth and feeding success of age-0 marine fishes are important prerequisites for overwinter survival (Sogard 1997, Sogard & Olla 2000, Heintz & Vollenweider 2010) and subsequent recruitment success. Larvae and juveniles of both species must acquire sufficient prey in spring and summer to not only outgrow size-selective predation pressure (Heintz & Vollenweider 2010), but to also support energetic demands required for metamorphosis; this energetic demand may also delay somatic growth (Heintz & Vollenweider 2010). After metamorphosis, the subsequent fall season is spent acquiring lipid reserves that may enhance the probability of survival through their first winter (Sogard 1997, Sogard & Olla 2000, Siddon et al. 2011). Walleye pollock juveniles below a minimum size will not be able to depend on energetic reserves in the form of lipids and will therefore be forced to forage during times of scarce resources, exposing them to higher predation risks (Heintz & Vollenweider 2010). Thus, understanding dietary patterns and feeding success of pelagic larvae and juveniles during the first growing season is of importance to better understand patterns of overwinter survival and recruitment success of these two important groundfish species in the southeastern Bering Sea.

In the southeastern Bering Sea, the broad continental shelf is seasonally differentiated into three bathymetrical regions, the Inner, Middle, and Outer Domains, which are separated by hydrographic fronts or transition zones (Coachman 1986, Schumacher & Stabeno 1998). Temperature and salinity are the strongest drivers of the location and strength of these fronts (Danielson et al. 2011). The shallow Inner Domain is unstratified due to wind and tidal mixing of the whole water column and is separated from the Middle Domain by the Inner Front, which is usually located near the 50m isobath (Stabeno et al. 2001, Kachel et al. 2002). The Middle domain is a two layered system, with an upper mixed layer separated from a deeper layer by a seasonal pycnocline at 15-40 m water depth. The Middle Front, usually located near the 100 m isobath, separates the Middle from the Outer Domain, which extends to waters of 200 m depth above the continental slope. This front consists of a wind mixed surface layer and a tidally mixed bottom layer, separated by a transition zone. Physical anomaly boundaries in the southeastern Bering Sea typically coincide with biophysical boundaries (Danielson et al. 2011), so it is reasonable to assume that distributional patterns of early life stages of walleye pollock and Pacific cod and their zooplankton prey may adhere to physical patterns as well. Consequently, this study examined and compared dietary patterns and feeding success of both gadids by domain and water depth.

The prevalent hypothesis predicting variability in walleye pollock recruitment in the southeastern Bering Sea is the Oscillating Control Hypothesis, OCH (Hunt et al. 2002, revised in Hunt et al. 2011). The revised OCH postulates bottom-up controls on walleye pollock recruitment during very warm periods, resulting in reduced recruitment success. Increased cannibalism and overwinter starvation in warm years is thought to be due to a lack of quality prey items, namely larger zooplankters such as the copepod *Calanus marshallae* and euphausiids (Coyle et al. 2011). For example, a comparison of the mid-shelf zooplankton communities in a cold (1999) and a warm year (2004) revealed a dramatic shift from large *(Calanus marshallae, Thysanoessa* spp.) to small *(Pseudocalanus* spp., *Oithona* spp.) zooplankton species (Coyle et a1. 2008, Pinchuk & Coyle 2008). A concurrent dietary shift from large to small copepods was also observed for age-0 walleye pollock, which was accompanied by a significant reduction in fish body size, with smaller juvenile walleye pollock occurring in the cold year (Coyle et al. 2008). Despite the smaller size of walleye pollock in cold 1999, substantially more larger prey items were contributing to their diet relative to that of the larger fish in warm 2004 (Coyle et al. 2008, Coyle et al. 2011). Since differences in the feeding success of walleye pollock are presumably related to prey availability, it is likely that the lack of large prey in warm 2004 may have resulted in food limitations for juvenile walleye pollock and the co-occurring juvenile stages of Pacific cod. The observed variability in feeding success emphasizes the importance of gaining a better understanding of the factors influencing these fishes at a time when they are trying to grow out to a suitable overwintering size.

The southeastern Bering Sea experiences oscillating temperature regimes (Overland & Stabeno 2004, Mueter & Litzow 2008) which in turn affect sea ice conditions (i.e., extent, coverage, thickness, and seasonality), water temperature, and stratification in this region. These changes in the physical environment will likely influence the timing, duration, and magnitude of the spring bloom as well as recruitment success, growth, and nutritional condition of the entire zooplankton community (Walsh & McRoy 1986, Hunt et al. 2002, Hunt & Stabeno 2002, Hunt et al. 2011) and of the larval and juvenile walleye pollock and Pacific cod relying on that zooplankton community for prey (Coyle et al. 2011, Hunt et al. 2011). Determining feeding success and dietary overlap will allow us to compare and quantify patterns of resource allocation and the probability of feeding competition between early life stages of walleye pollock and Pacific cod. Seasonal sampling for this study was conducted in 2008, a year characterized by heavy ice cover, late ice retreat, and cold temperatures (Coyle et al. 2008). These conditions may have affected the abundance and composition of available prey for larval and juvenile walleye pollock and Pacific cod. The overall goal of this study was therefore to examine feeding success and dietary patterns of walleye pollock and Pacific cod during cold conditions in the southeastern Bering Sea and to assess the potential for dietary competition between larval and juvenile stages of these two commercially important groundfish species. The underlying hypothesis was that larvae and juveniles of these two species, which share ecological preferences, may feed on similar prey items and that these prey items may be limited during cold conditions, which may lead to dietary competition. Specifically, the objectives and testable hypothesis were:

1) Identify feeding patterns of age-0 walleye pollock and Pacific cod in the southeastern Bering Sea.
2) Examine prey composition in the diet of both species.
3) Compare feeding success and dietary composition of age-0 walleye pollock and Pacific cod from the exceptionally cold summer in 2008 to literature values to evaluate environmental effects on recruitment potential for these species.

My overarching null hypothesis for these objectives was that there are no significant difference in feeding success and dietary composition between larval and juvenile walleye pollock and Pacific cod.

METHODS AND MATERIALS

Sample collection

This study was based on samples of early life history stages of walleye pollock and Pacific cod that were acquired opportunistically from multiple projects and agencies (Table 1). The goal of sample acquisition was to obtain a good seasonal coverage of age-0 larval and juvenile stages of both species. Early life stages were obtained from sampling efforts in spring (May), summer (July), and fall (September) of 2008.

In spring of 2008, pre-flexion larvae were collected by the Alaska Fisheries Science Center, National Marine Fisheries Service (AFSC, NMFS; Figure 1). Fish larvae were collected with vertical 60 cm diameter Bongo tows equipped with 335 μm mesh net.

Sampling was conducted 24 h a day. However, only samples received from two stations were sampled after dusk. After retrieval of the sampling gear, all fish larvae were removed from the codend and preserved in 5 % buffered formalin seawater solution. Six walleye pollock and 8 Pacific cod larvae still had retained a yolk-sac and were therefore considered to be not yet actively feeding; consequently, these fish were excluded from all subsequent calculations of feeding success and diet composition.

In the summer of 2008, samples of pelagic flexion larvae were obtained by the University of Alaska Fairbanks, School of Fisheries and Ocean Sciences (UAF, SFOS) during a cooperative research cruise conducted as a part of the Bering Ecosystem Study, National Science Foundation (BEST, NSF) and the Bering Sea Integrated Ecosystem Research Project, North Pacific Research Board (BSIERP, NPRB; Figure 2). Ichthyoplankton was collected using a $1 m^2$ Multiple Opening/Closing Net and Environmental Sensing System (MOCNESS; Wiebe et al. 1976) fitted with black 500 µm mesh net bags. The oblique MOCNESS tows provided depth-stratified samples in 20 m increments from a depth of 100 m, or near the bottom, to the surface. After retrieval of the sampling gear, flexion larvae were preserved for further laboratory analysis as described above.

In the fall, samples of pelagic juveniles of walleye pollock and Pacific cod were provided by the Bering Aleutian Salmon International Survey (BASIS) conducted by the Ted Stephens Marine Research Institute, National Oceanic and Atmospheric Administration (TSMRI, NOAA). Fish were collected with surface (0-20 m) and with midwater rope trawls that were used to target acoustic signals. Sampling methods are described in more detail by Moss et al. (2009). After retrieval of the gear, fish were identified to species and fixed in 5% sea water buffered formalin. Due to the low sample size, demersal juvenile Pacific cod were also received from the Fisheries Oceanographic Cooperative Investigations (FOCI) at the AFSC, NMFS (cruise number 3MF08; Figure 3); fish were collected with a beam trawl and recovered juveniles were frozen at sea for later processing.

Laboratory analyses

In the laboratory, all spring and summer fish were measured with calibrated microphotographic software to the nearest 0.1 mm standard length (SL), while fall samples were measured with a fish board to the nearest 1.0 mm fork length (FL). For each season, three size classes were identified based on the 33rd and 66th percentiles of the fish length frequency distributions of either species (Table 2). For each fish, the intestinal tract was excised and the stomach removed. Stomach fullness was visually estimated as (1) empty, (2) traces, and (3-6) 25%, 50%, 75%, and 100% full (Adams et al. 2007). Stomach contents were gently removed and ingested prey items were examined with a LEICA MZ 16 stereo microscope and a LEICA DM LB2 compound microscope. Prey items were identified to the lowest taxonomic level and developmental stage possible. Total prey wet weight was determined by multiplying an average prey taxon wet weight, obtained from zooplankton data collected from their respective cruises, by the number of that specific prey taxon in the gut. Spring zooplankton data did not include average biomass estimates; therefore, volume estimates (%V as a substitute for %W) were calculated using established mensuration formulas (Napp et al. 1999). Literature values for prey size estimates were taken as both mean carapace length and total length to calculate the mean total length (TL) of prey ingested.

Statistical analyses

For each season, cumulative prey curves were used to determine the number of stomachs needed to properly describe the dietary breadth of age-0 walleye pollock and Pacific cod (Treloar et al. 2007); all stomachs were randomized 10,000 times to reduce the potential for bias due to sampling order and the mean number of new prey categories was plotted against the total number of stomachs analyzed. If the curve reached an asymptote, it was assumed that the minimum sample size needed to adequately describe the diet of age-0 walleye pollock and Pacific cod had been met. Feeding success for all non-empty stomachs was described as numerical feeding intensity (the total number of prey items per stomach), and a fullness index (visually assigned values 1-6) (Adams et al. 2007). Feeding incidence (the proportion of fish with at least one item ingested) was described for all stomachs (Dauvin & Dodson 1990). Pairwise t-tests were used to test for significant differences in mean numerical feeding intensity, fullness, and prey size between size strata, domains, and depth strata within seasons.

Prey composition was expressed as percent number (%N), percent of total prey volume (%V) or percent of total prey weight (%W), and percent frequency of occurrence (%FO) from all non-empty stomachs (Cortés 1997). Finally, the percentage index of relative importance (%IRI) was calculated from the previous indices (Cortés 1997). Dietary comparisons were made with PRIMER Version6 (Clarke & Gorley 2006). Non-metric multi-dimensional scaling ordination (MDS) was used to visualize significant dietary differences by species, size class, domain, and depth. This approach employed a Bray-Curtis similarity coefficient matrix applied to either square or fourth-root transformed dietary data, depending on the degree of variance, and allowed for visualization of these dietary comparisons. Kruskal's stress statistic 1 (Clarke & Gorley 2006) was used to determine the best spatial representation of the samples. A stress of <0.2 was considered an acceptable fit (Clarke & Gorley 2006). Multivariate one-way analysis of similarities (ANOSIM) was used to investigate whether dietary composition differed significantly between size classes, domains, depth strata (within species and where applicable), and overall between species (Clarke & Gorley 2006). ANOSIM reports a global statistic that is analogous to an ANOVA, indicating whether or not to pursue pairwise tests. Similarity percentages (SIMPER) were used to isolate dietary categories that were significantly important, or contributed most to observed dissimilarities. Differences in dispersion, as a measure of diet variability, across groups were tested for significance using a permutation-based procedure (PERMDISP).

RESULTS

Spring

Twenty three prey types (Appendix A), which were pooled into 14 categories, were identified in the stomachs of pre-flexion walleye pollock and Pacific cod larvae. Ten of these categories occurred in either walleye pollock or Pacific cod stomachs.

Pre-flexion Walleye Pollock

All pre-flexion walleye pollock larvae (N=54) were assigned to three size classes (Table 2). A cumulative prey curve reached an asymptote at approximately 45-50 stomachs (Figure 4). Pre-flexion walleye pollock had an overall feeding incidence of 67.0%. The mean fullness index score was 2.7 (SD=1.2) (~18% full), the mean number of prey items ingested was 1.8 per stomach (SD=1.5) and the mean volume of ingested prey was 0.3 ml (SD=0.1).

Feeding success and dietary composition in pre-flexion walleye pollock larvae varied with size class. Feeding incidence increased with size from 42.2% in the smallest size class to 81.3% and 80.0% in size classes 2 and 3. Larvae from size class 2 were ingesting prey items with a significantly larger volume than both size classes 1 and 3 (Appendix B; Table 3). There were no significant differences in mean prey volume ingested by size class 1 and size class 3. Mean fullness was significantly higher in size class 2 than in size class 1 (Appendix B; Table 3). There was no significant difference in mean fullness between size classes 1 and 3 or between size classes 2 and 3. Mean numerical feeding intensity was 1.7 items per stomach (*SD*=1.5) and did not vary with size.

Pre-flexion walleye pollock larvae predominantly ingested developmental stages of pelagic copepods (Table 4). In the smallest size class, the diet consisted mainly of naupliar stages of *Pseudocalanus* spp. and *Metridia pacifica* and, to a lesser degree, of copepod eggs. Larvae in size class 2 switched to later naupliar stages of these two calanoid copepods; no copepod eggs were ingested. The diet in the largest size class was similar to that of size class 1, with the addition of larger amounts of copepod eggs and diatoms. Size class dietary compositions were not significantly different at the global level (1-way ANOSIM, Table 5). There were no significant differences in dietary dispersion by size class (PERMDISP, Table 5).

Feeding incidences reached 71.4% in both the Inner and Middle domains, but decreased to 60.0% in the Outer Domain. There were no significant differences in mean prey volume, mean fullness, or mean number of prey items ingested between any two domains in the spring season (Appendix B; Table 3), indicating that rearing habitat had little influence on the diet or larval walleye pollock.

The diet of walleye pollock larvae in the Inner and Middle domains consisted mainly of naupliar stages of *M. pacifica* and *Pseudocalanus* spp., as well as diatoms and barnacle cyprid larvae (Table 6). Larvae in the Outer Domain had similar majority dietary components, with the addition of copepod eggs. Dietary composition was not significantly different between domains (1-way ANOSIM, Table 5) and there were no significant differences in dietary dispersion (PERMDISP, Table 5).

Pre-flexion Pacific Cod

All pre-flexion Pacific cod larvae (N=47) were assigned to three size classes (Table 2). A cumulative prey curve reached an asymptote at approximately 35-40 stomachs (Figure 5). Pre-flexion Pacific cod larvae had an overall feeding incidence 71.8%. The mean fullness index score for all non-yolk-sac fish was 3.3 (SD=1.4) (~32.5% full), the mean number of prey items ingested per stomach was 2.0 (SD=0.8) and the mean volume of ingested prey was 0.5 ml (SD=0.3).

Feeding patterns in Pacific cod were a function of size. Feeding incidence increased from 33.3% in the smallest size class to 80.0% and 86.7% in size classes 2 and 3. Mean prey volume ingested by the largest size class was significantly larger than in size class 2 (Appendix B; Table 7). There were no other significant differences in mean prey volume by size class. Mean fullness was significantly higher in size class 3 than in size class 1 and size class 2 (Appendix B; Table 7). There was no significant difference in mean fullness between size classes 1 and 2. The mean number of prey items ingested was significantly higher in size class 3 than in size class 1 (Appendix B; Table 7), there were no other significant differences in the mean number of prey items ingested.

Similar to walleye pollock larvae, the diet of Pacific cod larvae consisted mostly of developmental stages of pelagic copepods. In contrast to walleye pollock, Pacific cod also included large proportions of copepodite stages into their diet (Table 8). Pacific cod in the smallest size class ingested mainly copepod eggs and early copepodite stages of *Calanus marshallae*, while larvae in size class 2 concentrated on copepod eggs and late naupliar stages of *M. pacifica* and *Pseudocalanus* spp. The diet in size class 3 was mainly comprised of late *M. pacifica* nauplii and early copepodite stages of both *C. marshallae* and *M. pacifica*; these fish also ingested calyptopis stages of euphausiids. There were no significant differences in either dietary composition (1-way ANOSIM) or dispersion (PERMDISP) across size classes in Pacific cod larvae (Table 5).

Other than feeding incidence, rearing habitat had little impact on feeding patterns in Pacific cod larvae. Feeding incidence in Pacific cod varied from a high in the Inner Domain at 90.0% to a low in the Middle Domain at 42.9% and 72.9% in the Outer Domain, but there were no significant differences in mean prey volume between any pair of domains (Appendix B; Table 7). Feeding incidence patterns may have been influenced by size class distributions, as there were no fish from size class 3 in the Middle Domain. Mean fullness was significantly higher in the Inner Domain than in the Middle Domain, but there were no other significant differences in mean fullness (Appendix B; Table 7). There were no significant differences in the mean feeding intensity by domain, with an average of 2.0 items per stomach (*SD*=0.8).

The diet of Pacific cod in the Inner and Outer domains consisted mainly of late *M. pacifica* nauplii and early *C. marshallae* copepodites (Table 9). Late *Pseudocalanus* spp. nauplii and copepod eggs were the only prey items identified from the Middle Domain. There were no significant differences in Pacific cod dietary composition (1-way ANOSIM) or dispersion (PERMDISP) by domain (Table 5).

Spring Summary

In spite of their spatial and temporal co-occurrence in spring of 2008 (Figure 1), larval stages of walleye pollock and Pacific cod showed clearly disparate patterns in feeding success and prey composition. Pacific cod larvae had a significantly higher prey volume and mean fullness score (Table 10) than walleye pollock larvae, but there was no significant difference in the mean number of prey per stomach between larval stages of both species. The overall dietary composition (Table 11) between pre-flexion walleye pollock and Pacific cod was significantly different (1-way ANOSIM, Table 5, Figure 6);

specifically, SIMPER analysis attributed these differences primarily to a higher consumption of copepod eggs and late stage *M. pacifica* nauplii by Pacific cod, while walleye pollock were consuming higher numbers of smaller and younger naupliar stages, namely *M. pacifica* and *Pseudocalanus* spp. There was no significant difference in dietary dispersion between walleye pollock and Pacific cod larvae in the spring (PERMDISP, Table 5).

Summer

Thirty five prey types (Appendix A) pooled into 17 categories were identified in the stomachs of flexion walleye pollock and Pacific cod collected in the summer of 2008; of these, 13 occurred in the diet of flexion walleye pollock, while only eight categories were found in the diet of flexion Pacific cod larvae.

Flexion Walleye Pollock

All flexion larvae (N=113) were separated into three size classes (Table 2). A cumulative prey curve reached an asymptote at approximately 50 stomachs (Figure 7). Walleye pollock larvae had an overall feeding incidence of 79.6% and a mean fullness index score of 3.4 (*SD*=1.2) (~35% full). Mean number of prey items ingested was 6.5 per stomach (*SD*=5.3) and the mean size of ingested prey items was 0.9 mm (*SD*=0.5).

Feeding success and prey composition varied with larval size, with feeding incidence increasing from 69.2% in the smallest size class to 81.5% and 87.2% in size classes 2 and 3, respectively. Larvae from size class 1 were ingesting prey items with a significantly smaller mean size than larvae from either size classes 2 or 3 (Appendix B, Table 12). Larvae from size class 3 were ingesting prey with a significantly larger mean size than fish in size class 2. There were no significant differences in mean fullness between size classes. Both size classes 2 and 3 were ingesting a higher mean number or prey items than size class 1 (Appendix B, Table 12), but there was no significant difference in the mean number of prey items per stomach between size classes 2 and 3.

Similar to the spring dietary composition, walleye pollock flexion larvae continued to consume mostly developmental stages of copepods (Table 13). The diet of walleye pollock in the smallest size class consisted mainly of late naupliar and varying copepodite stages of *Pseudocalanus* spp. Larvae in size class 2 switched to a more copepodite-dominated diet consisting mainly of *Acartia longiremis* and *Pseudocalanus* spp., while fish of size class 3 also added *C. marshallae, Neocalanus* spp., and *Oithona similis* copepodites. Dietary composition significantly differed between size classes at the global level (1-way ANOSIM, Table 14, Figure 8). Subsequent pairwise comparisons were significantly different between all size classes. SIMPER analysis indicates that these differences were primarily due to higher consumption of *Pseudocalanus* spp. nauplii by size class 1, of *A. longiremis* and *Pseudocalanus* spp. copepodites by size class 2, and of

O. similis and the latest copepodite stages of *A. longiremis* and *Pseudocalanus* spp. by size class 3. There were no significant differences in dietary dispersion between size classes (PERMDISP, Table 14).

Rearing habitat also affected feeding patterns, with feeding incidence increasing with distance from the coast from 75.0% in the Inner Domain to 80.0% in the Middle Domain; fish in the Pribilof Island area had the highest feeding incidence with 89.5%. Mean prey size was significantly higher in the Inner Domain and Pribilof Island area than in the Middle domain (Appendix B, Table 12), but there was no significant difference in mean prey size between the Inner Domain and Pribilof Island area. There were no significant differences in mean fullness or mean number of prey items ingested by domain in the summer season.

The diet of walleye pollock in the Inner Domain consisted mainly of copepodite stages of *Pseudocalanus* spp., *A. longiremis,* and *O. similis*, while late *Pseudocalanus* spp. nauplii and copepodite stages of *O. similis* were the most important component of the diet in the Middle Domain (Table 15). In the Pribilof Island area, late naupliar and copepodite stages of *Pseudocalanus* spp. and *A. longiremis* copepodites dominated the diet. Dietary composition was significantly different between domains at the global level (1-way ANOSIM, Table 14, Figure 9); subsequent pairwise comparisons revealed a significant difference between the Inner Domain and Pribilof Island area. SIMPER indicated that the mid to late stages of *O. similis* most consistently contributed to the overall differences between domains. There were no significant differences in dietary dispersion between domains (PERMDISP, Table 14).

Depth-stratified sampling in summer allowed for a comparison of feeding patterns by depth. Feeding incidence in walleye pollock increased from 84.0% in the 0-20 m depth layer to 100% in the 20-40 m layer, to a low of 75.0% in the 40-60 m depth layer. Mean prey size was significantly higher in both the 20-40 and 40-60 m than in the 20-0 m depth layer (Appendix B, Table 12), there was no significant difference in mean prey size between the 20-40 m and 40-60 m layers. Mean fullness was significantly higher in the 20-40 m layer than in the surface layer (Appendix B, Table 12); no other fullness comparisons were significant. There were no significant differences in numerical feeding intensity between any pairs of depth layers.

The diet of walleye pollock in the surface layer consisted mainly of late naupliar stages of *Pseudocalanus* spp. along with late copepodite stages of *Pseudocalanus* spp. and *A. longiremis* (Table 16). In contrast, late *Pseudocalanus* spp. copepodites dominated the diet in the 20-40 m depth layer, while copepodite stages of *Pseudocalanus* spp. and *O. similis* contributed most to the diet in the 40-60 m depth layer. Depth had no significant effect on dietary composition at the global level (1-way ANOSIM, Table 14). There were no significant differences in the overall dietary dispersion between depth layers (PERMDISP, Table 14).

Flexion Pacific Cod

The low sample size of Pacific cod flexion larvae in the summer (n=5) allowed for only very restricted data analysis. Additionally, one larva contained no identifiable prey, effectively reducing the sample size to four. Pacific cod ranged in size from 9.1 to 16.4 mm SL. Due to the low sample size, no size classes were identified in this season. A cumulative prey curve was constructed, but failed to reach an asymptote (Figure 10). Pacific cod flexion larvae had an overall feeding incidence of 100%. The mean fullness index score of 4.4 (SD=2.2) (~60.0% full), the mean number of prey items ingested was 5.0 per stomach (SD=4.1) and the mean prey size was 1.7 mm (SD=1.7).

Feeding incidence in Pacific cod was constant across all domains and depth layers at 100%. Prey size did not differ significantly with domains or depth layers. There were no significant differences in mean fullness between any pair of domains or depth layers and no significant differences in feeding intensity between any pair of domains or depth layers.

The diet of Pacific cod was similar across domains and depth layers due to the small sample size (Table 1). PRIMER analyses within summer Pacific cod samples could not be conducted in a meaningful manner.

Summer Summary

Despite the low sample size for Pacific cod flexion larvae in the summer of 2008, comparisons of feeding patterns between both species still revealed some notable differences (Table 17). Mean prey size was significantly higher in Pacific cod than in walleye pollock larvae (Table 10), but there was no significant difference in mean fullness score or in the mean numerical feeding intensity between larval walleye pollock and Pacific cod. The overall dietary composition between flexion walleye pollock and Pacific cod larvae was significantly different (1-way ANOSIM, Table 14, Figure 11) and SIMPER analysis indicated that these differences were primarily due to a higher Pacific cod consumption of adult *Pseudocalanus* spp., early *C. marshallae* copepodites, late *Neocalanus cristatus* copepodites, and *Neocalanus* spp. nauplii. In contrast, walleye pollock were consuming higher numbers of late copepodite *A. longiremis* and mid-stages of *Pseudocalanus* spp. There was no significant difference in dietary dispersion between walleye pollock and Pacific cod larvae (PERMDISP, Table 14).

Fall

In the stomachs of juvenile walleye pollock and Pacific cod, 21 prey (Appendix A) types pooled into 15 categories were identified; of these, 14 occurred in the diet of either target species.

Juvenile Walleye Pollock

All juvenile walleye pollock (N=62) were assigned to 3 size classes (Table 2). The cumulative prey curve reached an asymptote at around 20 stomachs (Figure 12). Juvenile walleye pollock had an overall feeding incidence of 95.2%, a mean fullness index score of 3.9 (*SD*=1) (~48.0% full), the mean number of prey items ingested was 74.7 per stomach (*SD*=98.4) and the mean prey size was 2.1 mm (*SD*=2.5).

Feeding incidence in walleye pollock increased with size from 88.9% in the smallest size class to 100% in size classes 2 and 3. Juveniles from size class 1 were ingesting prey items with a significantly smaller mean size than both size classes 2 and 3 (Appendix B; Table 18). There was no significant difference between mean prey size ingested by size classes 2 and 3. There were no significant differences in mean fullness and in the mean number of prey items ingested between size classes.

Size had no apparent effect on dietary composition in juvenile walleye pollock. The diet across all size classes consisted mainly of mature *Pseudocalanus* spp., *C. marshallae* copepodites, juvenile euphausiids, and chaetognaths (Table 19). There was no significant difference in dietary composition between size classes at the global level (1-way ANOSIM, Table 20). There were no significant differences in dietary dispersion by size class (PERMDISP, Table 20).

Feeding incidence in the Inner and Outer Domains was 100%, and fell to 88.0% in the Middle Domain. Mean prey size was significantly higher in the Inner and Outer domains than in the Middle Domain (Appendix B; Table 18). There was no significant difference in mean prey size between the Inner and Outer domains. Juvenile walleye pollock in the Inner Domain were ingesting a significantly higher mean number of prey items than those in the Outer Domain and had a significantly higher mean fullness than both the Middle and Outer domains (Appendix B; Table 18). No other differences in the mean number of prey items or mean fullness were significant.

The diet of walleye pollock across domains consisted mainly of mature *Pseudocalanus* spp., copepodites of *C. marshallae*, juvenile euphausiids, and chaetognaths (Table 21). There were no significant differences in dietary composition between domains at the global level (1-way ANOSIM, Table 20). There was, however, a significant difference in dietary dispersion between domains at the global level (PERMDISP, Table 20) and subsequent pairwise comparisons revealed that dietary dispersion was significantly greater in the Middle than in the Inner Domain (Table 20).

Feeding incidence in walleye pollock juveniles fell from 100% in the surface layer, to 90.0% in the mid-water depth layer. Mean prey size was significantly higher in the mid-water depth layer (Appendix B; Table 18). Neither mean fullness nor mean number of prey items ingested varied significantly between depth layers.

The diet of walleye pollock in the surface layer consisted mainly of adult *Pseudocalanus* spp., copepodites of *C. marshallae*, and juvenile euphausiids. The diet in the mid-water layer was similar with the addition of chaetognaths (Table 22). Dietary composition did not vary between trawl depth layers in the global comparison (1-way ANOSIM, Table 23) and there was no significant difference in dietary dispersion between depth layers (PERMDISP, Table 23).

Juvenile Pacific Cod

All Pacific cod juveniles ($N = 42$) were assigned to three size classes (Table 2). A cumulative prey curve reached an asymptote at around 36 stomachs (Figure 13). All Pacific cod juveniles had an overall feeding incidence of 100% with a mean fullness index score of 4.3 (*SD* = 1.3) (~58.0% full) and the mean numerical feeding intensity was 11.4 items per stomach (*SD* = 16.9), with a mean prey size of 5.3mm (*SD*=3.7).

Feeding incidence in all Pacific cod size classes was 100%. The mean prey size ingested by size class 1 was significantly larger than in both size classes 2 and 3 (Appendix B; Table 24). There was no significant difference in mean prey size between size classes 2 and 3. While there were no significant differences in mean fullness between any pair of size classes, the mean number of prey items ingested was significantly higher in both size classes 2 and 3 than in size class 1 (Appendix B; Table 24).

In the smallest size class, diet consisted mainly of juvenile euphausiids (*Thysanoessa* spp.) and *Chionoecetes* spp. megalopae, while fish in size class 2 focused on developmental stages of euphausiids and late copepodite and adult stages of *C. marshallae* (Table 25). Pacific cod in size class 3 shared a similar diet with size class 2, with the addition of large numbers of the pteropod *Limacina helicina*. There was a significant difference in the dietary composition between size classes of juvenile Pacific cod at the global level (1-way ANOSIM, Table 20, Figure 14); subsequent pairwise comparisons revealed significant differences in dietary composition between all size classes (Table 20). SIMPER indicated that euphausiid juveniles, chaetognaths, and hyperiid amphipods most consistently contributed to compositional differences across size classes. Dietary dispersion did not differ significantly between size classes at the global level (PERMDISP, Table 20).

Pacific cod had a feeding incidence of 100% across all domains. Juveniles were ingesting larger prey in both the Middle and Outer domains than those in the Inner Domain (Appendix B; Table 24). Mean prey size ingested and mean fullness were significantly larger in the Outer than in the Middle Domain. The mean number of prey items ingested was significantly higher in the Inner Domain than in both the Middle and Outer domains (Appendix B; Table 24); there was no significant difference in the feeding intensity between the Middle and Outer Domains.

The diet of Pacific cod in the Inner Domain consisted mainly of developmental stages of euphausiids along with the pteropod *L. helicina* (Table 26). In contrast, the majority of the diet in the Middle Domain consisted mainly of late copepodite and adult stages of *C. marshallae,* juvenile euphausiids, *P. elegans,* and *T. pacifica.* All Outer Domain samples were from a single station, where *Chionoecetes* spp. megalopae dominated the diet of Pacific cod. Pacific cod dietary composition varied significantly between the Inner and Middle Domain (1-way ANOSIM, Table 20, Figure 15). SIMPER analysis indicated that the dietary abundance of juvenile euphausiids most consistently contributed to differences across domains. Dietary dispersion was significantly different across domains at the global level (PERMDISP, Table 20) and between all pairs of domains, with dispersion being greater in both the Inner and Middle Domains than in the Outer Domain (Table 20). Dietary breadth was significantly higher in the Middle Domain than in the Inner Domain.

Feeding incidence in Pacific cod juveniles was 100% across all depth layers. Mean prey size was significantly higher in the mid-water depth layer than in both the surface and bottom layers and also significantly larger in the surface than in the bottom depth layer (Appendix B; Table 24). There were no significant differences in mean fullness between any pair of depth layers. While feeding intensity did not vary between the surface and mid-water depth layers, juveniles collected from the bottom layer had significantly higher mean number of prey items ingested than those from either the surface or the mid-water layers (Appendix B; Table 24).

Dietary composition of Pacific cod juveniles was a function of capture depth (Table 27). The diet of Pacific cod in the surface layer consisted mainly of juvenile euphausiids and late copepodites and adults of *C. marshallae*. Juveniles collected from the mid-water contained *Chionoecetes spp.* megalopae, which were never observed in fish from the surface or the bottom layer, as well as *T. pacifica* and *P. elegans*. The diet in the bottom layer consisted mainly of developmental stages of euphausiids; in addition, only these fish ingested notable numbers of the pteropod *L. helicina*. Juvenile Pacific cod dietary composition was significantly different between depth layers at the global level (1-way

ANOSIM, Table 23, Figure 16); subsequent pairwise comparisons revealed significant differences between the all pairs of depth layers (Table 23). Differences in dietary composition were primarily due to a lack of juvenile euphausiids and the presence of *Chionoecetes* spp. megalopae in the mid-water depth layer as well as the presence of pteropods in the bottom depth layer. No significant differences in dietary dispersion between depth layers were found (PERMDISP, Table 23).

Fall Summary

In the fall, dietary patterns were even more disparate between pelagic juvenile stages of walleye pollock and Pacific cod than earlier in the season. Specifically, mean prey size and mean fullness score (Table 10) were both significantly higher in juvenile Pacific cod than in walleye pollock. In contrast, walleye pollock juveniles had a significantly higher mean numerical feeding intensity than Pacific cod juveniles (Table 10). Differences in feeding success were also apparent in dietary composition (1-way ANOSIM, Table 23, Figure 17); according to SIMPER analysis, these differences were primarily due to higher consumption of late calanoid copepodites by juvenile walleye pollock, while Pacific cod juveniles consumed higher numbers of larger crustaceans, such as *Chionoecetes* spp. megalopae and the hyperiid amphipod *T. pacifica.* In addition, dietary dispersion was significantly higher in juvenile Pacific cod than in walleye pollock (PERMDISP, Table 23).

In the fall season, Pacific cod juveniles were not only collected from the surface and mid-water, but also with a bottom trawl. Importantly, all bottom trawl Pacific cod were sampled in the shallow Inner Domain. Since there were no walleye pollock processed from bottom trawl samples, analyses were repeated excluding Pacific cod sampled with the bottom trawl. All previously significant comparisons between walleye pollock and Pacific cod remained significantly different (α =0.05). Pacific cod mean prey size increased to 7.1mm (*SD*=5.9), while the mean number of prey fell to 4.0 per stomach (*SD*=6.2). The mean visual fullness index was similar at 4.4 (*SD*=1.2). Analysis of similarities (1-way, R=0.6, $p \leq 0.001$) remained significantly different between walleye pollock and Pacific cod.

DISCUSSION

Feeding success of age-0 walleye pollock and Pacific cod in the southeastern Bering Sea was a function of size, domain, and depth of occurrence. Fish body size seemed to have the largest influence on feeding success, followed by depth and domain. There were considerable differences in feeding success by body size in every season, which was likely due to increases in mobility, perception, gape size, and energetic demands of age-0 fish as they grow (Webb & Weihs 1986, Devries et al. 1998, Porter & Theilacker 1999, Heintz and Vollenweider 2010). In summer, walleye pollock diet was also associated with depth of occurrence, possibly because their primary diet changes from copepod nauplii to copepodites. Copepod nauplii tend to reside in the surface layer , while later developmental stages begin to implement vertical diel migration (Batchelder 1985). It should be noted that depth-stratified samples were not available from the spring: therefore, it is impossible to assess potential differences in diet with depth of pre-flexion larvae. The establishment of fronts creates domains whose vertical structure and water mass characteristics differ (Danielson et al. 2011), which in turn may affect primary and secondary production and hence the composition of the zooplankton community that provides prey for larvae. As the year advanced, sample location over the continental shelf became more important. This was likely connected to the seasonal establishment of these transitional fronts which separate the domains and the inhabiting zooplankton communities.

Spring

It should be noted that a total of seven walleye pollock and four Pacific cod pre-flexion larvae were sampled outside of daylight hours and that all of these fish were collected in the Outer Domain; however, these fish contained identifiable prey items and had similar visual fullness index values when compared to fish collected between dawn and dusk. It is also worth noting that of these fish, there were no walleye pollock larvae from size class one and there were only Pacific cod larvae from size class three; however there were additional larvae from both species sampled in the Outer Domain spanning all size classes and collected during daylight hours.

Copepod nauplii are of primary importance in the diet of pre-flexion walleye pollock larvae. In samples collected during the spring of 2008, copepod nauplii accounted for approximately 88.0% of the diet. More specifically, late naupliar stages of *M. pacifica* and early naupliar stages of *Pseudocalanus* spp. were predominant in the diet. Similarly, *Metridia* sp. stage IV nauplii were also the most abundant prey for walleye pollock larvae collected in April in the southeastern Bering Sea during a relatively warm year in 1992 (Hillgruber et al. 1995). While other studies did not attempt to identify prey items to genus, it was still confirmed that copepod nauplii accounted for ~90.0% of the walleye pollock diet during the spring in another warm year in 1979 (Nishiyama et al. 1986). In the Gulf of Alaska, spring-time pre-flexion larvae were also found to be numerically concentrating (88.0-96.0%) on copepod nauplii (Canino et al. 1991). Similarly, copepod nauplii in the size range of 160-230μm, presumably belonging to *Pseudocalanus* spp. and *Oithona* sp., were the most abundant food item in walleye pollock larvae ≤ 14mm collected southwest of Kodiak Island (Kendall et al. 1987). Since these larvae were feeding in waters that were warm (5-7°C) in comparison to 2008 southeastern Bering Sea temperatures (~0°C), the compositional differences in the diet might be the result of differences in the thermal regimes.

Temperature regimes seem to have significant effect on feeding success of pre-flexion walleye pollock. Overall feeding success was much higher in the exceptionally warm spring of 1979 (Nishiyama et al. 1986) than during a moderately warm year in 1992 (Hillgruber et al. 1995) or during the cold year (Coyle et al. 2011) of this study (2008).

For example, overall feeding incidence in 1979 was 93.0%, compared to 57.0% in 1992 and 67.0% in 2008. Average numerical feeding intensity was also higher in warmer years, namely, 4.2-13.7 prey per stomach for larvae (3.5-9.5 mm SL) in 1979 (Nishiyama et al. 1986) and 1.3-6.1 prey per stomach for larvae (3.8-6.1 mm SL) in 1992 (Hillgruber et al. 1995), compared to a mean of 1.8 prey items per stomach for larval walleye pollock (3.2-7.4 mm SL) in this study. It should be noted, however, that greater feeding success in warmer years does not necessarily translate to an energetic advantage for walleye pollock larvae, since cold temperatures experienced by the fish in this study likely represent very different metabolic demands than those experienced during warmer conditions.

One other study identified prey items to species and stage, which allowed for a detailed compositional comparison between May in cold 2008 (Coyle et al. 2011) and a warmer year in April of 1992 (Hillgruber et al. 1995). The largest difference was a higher concentration of smaller-bodied copepod nauplii during the warmer spring of 1992. While later naupliar stages of *Metridia* sp. were the most abundant prey items in both studies, there were still some marked differences. In 1992, the smaller-bodied *Microcalanus* sp. and *O. similis* copepod nauplii were much more abundant in the diet of pre-flexion walleye pollock, while in cold 2008, *Pseudocalanus* spp. copepod nauplii accounted for nearly 36.0% of the diet numerically. These differences in prey item size might have been driven by structural changes in the zooplankton community due to different temperature regimes (Coyle et a1. 2008, Pinchuk & Coyle 2008). It should be noted that the 1992 study was conducted at one single station in the Middle Domain of the southeastern Bering Sea, while the present study incorporated samples from multiple locations across the Bering Sea shelf, thus allowing for a more widespread description of feeding habits. Nonetheless, differences between the 1992 study and results presented here are in agreement with predictions about the composition of the zooplankton community structure in different thermal conditions (Coyle et al. 2008).

This study provides the first available information on the diet of pre-flexion Pacific cod larvae in the southeastern Bering Sea. Larval Pacific cod diet in spring consisted mainly of late naupliar stages of *M. pacifica,* copepod eggs, and early copepodite stages of *C. marshallae.* While no other published data on pre-flexion Pacific cod diet in the southeastern Bering Sea were available, the diet of larval Pacific cod ≤5 mm SL in March and April in Mutsu Bay, Japan, was also restricted to mainly *Pseudocalanus* spp., *Oithona* spp., and *Metridia* spp. nauplii (Takatsu et al. 1995); larvae of 5-10 mm SL, while still consuming copepod nauplii, began to also incorporate copepodite and adult stages of *Pseudocalanus* spp., *Acartia clausi*, and *Oithona* spp. into their diet.

Spring dietary patterns of walleye pollock and Pacific cod revealed notable differences between co-occurring larval stages of both species. In the spring, although there was not a significant difference in mean numerical feeding intensity, larval Pacific cod were scored higher on the visual fullness index and were ingesting prey with a significantly larger mean volume than walleye pollock larvae. The dietary composition was also significantly different, mainly due to the abundance of late stage *M. pacifica* nauplii in the diet of larval Pacific cod, as well as other, comparatively larger prey types, such as euphausiid calyptopis. In contrast, larval walleye pollock were consuming a higher number of earlier stage *M. pacifica* and *Pseudocalanus* spp. nauplii. Although there was some degree of overlap, the overall composition of the diet was disparate enough to be significantly different.

Summer

Summer walleye pollock diet was dominated by late naupliar and copepodite stages of *Pseudocalanus* spp., as well as late copepodite stages of *A. longiremis*. While this was the first study to describe dietary patterns of flexion walleye pollock in the southeastern Bering Sea, the diet of larval walleye pollock from June of 1987 in the Gulf of Alaska demonstrated a strikingly similar dietary composition, with high abundances of *Pseudocalanus* spp. and *Acartia* sp. copepodites and adults (Grover 1990), even though these larvae were slightly larger (10-30 mm SL) than those examined in this study. This indicates that feeding patterns described here appear to be typical for walleye pollock flexion larvae. In contrast, Pacific cod flexion larvae in summer relied most heavily on late copepodite stages of *N. cristatus* and *Pseudocalanus* spp. in the southeastern Bering Sea. This was similar to the diet of Pacific cod flexion larvae in mid-August in near-shore waters of the Gulf of Alaska (Abookire et al. 2007). The diet of Pacific cod flexion larvae in the Gulf of Alaska was restricted to mainly unidentified calanoid copepodites, while smaller larvae in the 5-10 mm SL range still concentrated numerically on copepod nauplii, but began to incorporate copepodite stages as well. The range of ingested prey items in comparison to fish size range was similar to this study thus suggesting a preference of Pacfic cod flexion larvae for a somewhat larger prey size range than similar life stages of walleye pollock

Dietary composition was considerably different between flexion walleye pollock and Pacific cod during the summer season. While larval Pacific cod were ingesting prey with a larger mean size than walleye pollock larvae, no significant differences were found in mean numerical feeding intensity or fullness. Dietary composition was also significantly different, most notably due to the presence of late developmental stages of the large copepod *N. cristatus* in the larval cod diet, as well as other large prey types such as the hyperiid amphipod *T. pacifica*. In contrast, walleye pollock flexion larvae continued to consume higher numbers of comparatively smaller prey items, such as *Pseudocalanus* spp. and *A. longiremis* copepodites. While the number of Pacific cod larvae available for this study was low, the differences in dietary patterns between the two species were still notable enough to be statistically significant, suggesting a notable difference in resource use despite an overlap in spatial and temporal distribution of early life stages of both species.

Fall

In the fall, juvenile walleye pollock relied most heavily on *Pseudocalanus* spp. adults, adult and late copepodite stages of *C. marshallae,* the chaetognath *P. elegans,* and juvenile euphausiids, similar to diets observed during other cool years in the southeastern Bering Sea (Moss et al. 2009, Coyle et al. 2011). These can be contrasted with juvenile walleye pollock diets during several warm years in the southeastern Bering Sea (Schabetsberger et al. 2000 & 2003, Moss et al. 2009, Coyle et al. 2011). While comparisons of feeding success were not available as most previous studies combined the prey items from multiple fish before identification, it was nonetheless possible to compare dietary composition. The most important difference was a numerical prevalence of small copepods in warm years, in some instances reaching 80.0-99.0% of the total diet (Schabetsberger et al. 2000 & 2003). While euphausiids were always present in the diet of juvenile walleye pollock, euphausiid juveniles reached 27.0% of the total dietary weight in the cold year of 2008, second only to the dietary weight of *C. marshallae* which accounted for >40.0% of the total. In the warm years of 2003-2005, cannibalism was observed in the diet of juvenile walleye pollock, reaching >20.0% of the total weight of prey items in 2003 (Coyle et al. 2011). Conversely, not one instance of cannibalism was encountered in this study. However, further study is needed to clarify if intracohort cannibalistic behavior in juvenile walleye pollock prior to their first winter is the result of high juvenile density and large size disparity or due to the lack of other adequate prey resources. While the small-bodied copepod *Pseudocalanus* spp. was present in the diet of juvenile walleye pollock in this study, it did not reach the peak abundance of small copepods observed in warmer years (Schabetsberger et al. 2000 & 2003). Additionally, the numbers of the large-bodied copepod *C. marshallae* encountered in the diet of walleye pollock in this study were much greater than those in warmer years

(Schabetsberger et al. 2000 & 2003, Coyle et al. 2011). These results clearly support the conclusions of Coyle et al. (2008 & 2011) that dietary composition of walleye pollock juveniles in the fall seems to be strongly influenced by the governing temperature regime.

In the fall, the diet of juvenile Pacific cod consisted mostly of developmental stages of euphausiids. Only one station in the Outer Domain that contained predominately fish of size class 1 represented an exception to this pattern by including *Chionoecetes* spp. megalopae in the diet. While there were significant differences in dietary composition between both size classes and domains, SIMPER analysis did not indicate that *Chionoecetes* spp. megalopae were majority contributors to these differences. While no other published data on the diet of fall juvenile Pacific cod in the southeastern Bering Sea are available the diet of juvenile Pacific cod in mid-August in near-shore waters of the Gulf of Alaska consisted mainly of calanoid copepodites (Abookire et al. 2007). As fish size increased, juvenile Pacific cod began to incorporate mysids and amphipods into their diet as well (Abookire et al. 2007). The relationships between predator size and prey item size range were similar to the results of this study. In contrast to this study, Abookire et al. (2007) sampled the nearshore environment, hence Pacific cod juveniles in these two studies were likely exposed to and feeding on very different zooplankton communities and this was apparent in their diets.

Differences in feeding patterns between walleye pollock and Pacific cod were most apparent in the fall. Mean prey size and fullness index were both notably higher in Pacific cod juveniles, while walleye pollock juveniles were consuming greater numbers of comparatively smaller prey items. The dietary composition was also markedly different, primarily due to the increased number of large crustacean type prey items ingested by Pacific cod. Juvenile walleye pollock, in contrast, continued to consume large numbers of adult and copepodite stages of calanoid copepods. Since no juvenile walleye pollock were processed from Inner Domain bottom trawl samples, comparisons were made excluding the FOCI bottom trawl Pacific cod. While this did influence mean prey size and numerical feeding intensity in Pacific cod, it did not influence the results of the species comparisons.

CONCLUSION

In spite of the temporal and often spatial co-occurrence of age-0 walleye pollock and Pacific cod, the overall feeding patterns of larvae and juveniles were found to be significantly different in every season, both in terms of feeding success and dietary composition. These dietary differences suggest a form of prey partitioning and therefore indicate that competition for prey between early life stages of these two gadoid fishes is unlikely to occur, at least during cold conditions as experienced in 2008 in the southeastern Bering Sea.

Diets of walleye pollock early life stages also differ notably between cold and warm years. Specifically, a preference for large-bodied copepods during cold conditions as experienced in 2008 was observed in this study, while the diet was found to be dominated by smaller bodied copepods in warmer years (Hillgruber et al. 1995, Schabetsberger et al. 2000 & 2003, Coyle et al. 2011). In warmer years, larger walleye pollock juveniles in the fall also displayed at least some degree of cannibalism (Coyle et al. 2011) whereas I found no evidence of cannibalism in this study. Nonetheless, our results support the idea that changing thermal conditions have a marked impact on feeding success and dietary composition of larvae and juveniles of walleye pollock prior to their first winter in the southeastern Bering Sea.

This was the first study to explore feeding success and dietary composition of age-0 larvae and juveniles of Pacific cod in the southeastern Bering Sea. Thus, results from this study are a valuable first step in exploring the potential impact of changing thermal conditions on the feeding patterns of early life stages of this important groundfish prior to their first winter. The scarcity of data on Pacific cod diets in the southeastern Bering Sea currently precludes predictions about the impacts of a changing ocean climate on the condition, growth, and survival of early life stages of Pacific cod.

My results indicate prey partitioning and therefore an avoidance of competition between co-occurring larval and juvenile walleye pollock and Pacific cod during cold conditions in the southeastern Bering Sea. While Pacific cod demonstrated a preference for fewer, larger-bodied prey items, especially in the fall, juvenile walleye pollock met their increasing metabolic demands by consuming increasing numbers of calanoid copepods.

One potential explanation for this prey size difference is that Pacific cod may have a larger gape size than walleye pollock at similar body sizes. If warmer temperatures are associated with a decline in the abundance of large zooplankton species (Hunt et al. 2011, Coyle et al. 2011), it is possible that the diets of these two fishes would converge or that Pacific cod might even exert predation pressure on walleye pollock directly. These scenarios, which could have dramatic impacts on the recruitment success for these important groundfish species, warrant further exploration, particularly under expected warming in the sub-arctic waters of the southeastern Bering Sea.

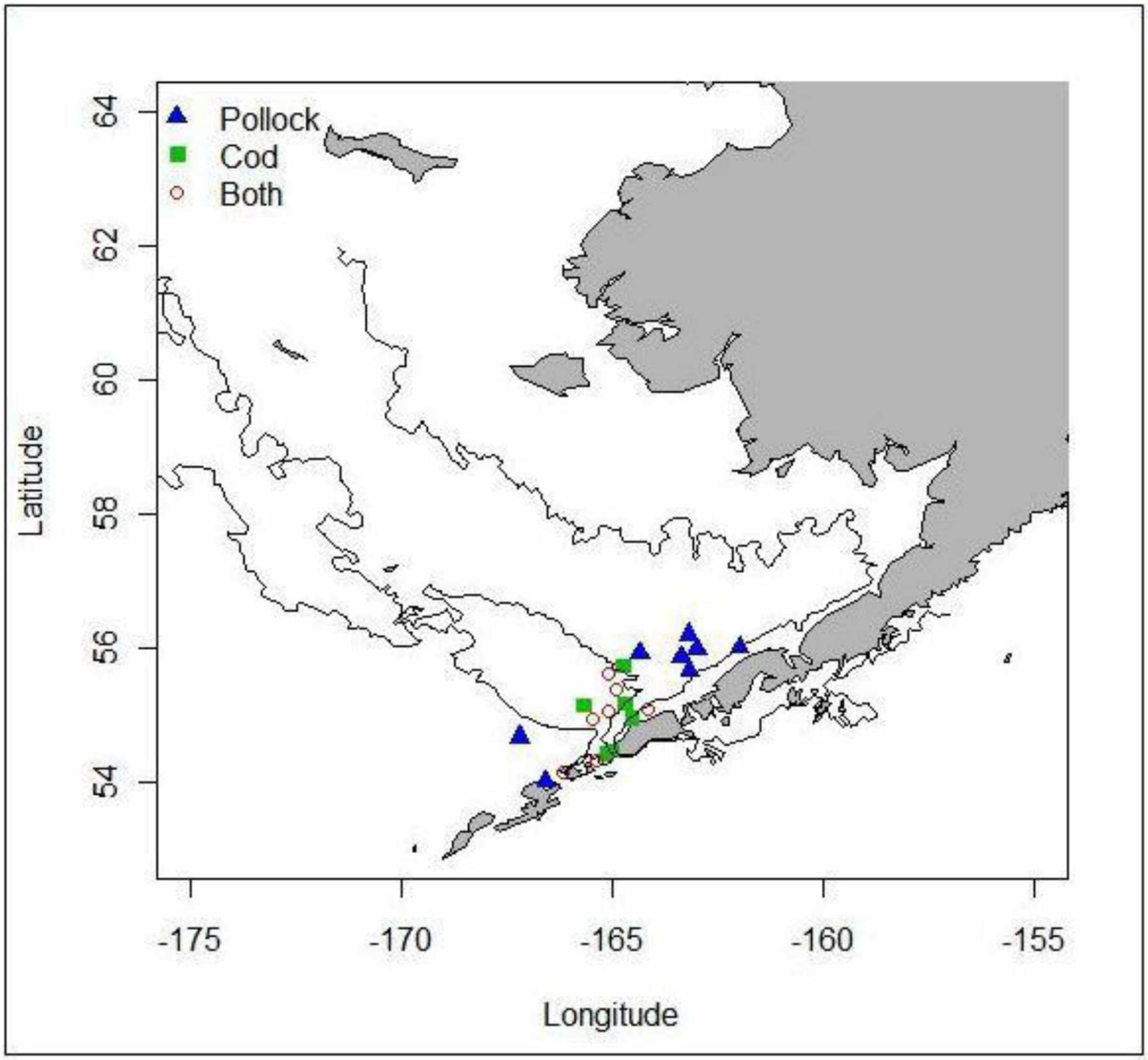

Figure 1. Sampling sites for pre-flexion walleye pollock and Pacific cod larvae from the FOCI 3DY08 cruise in the southeastern Bering Sea in May, 2008.

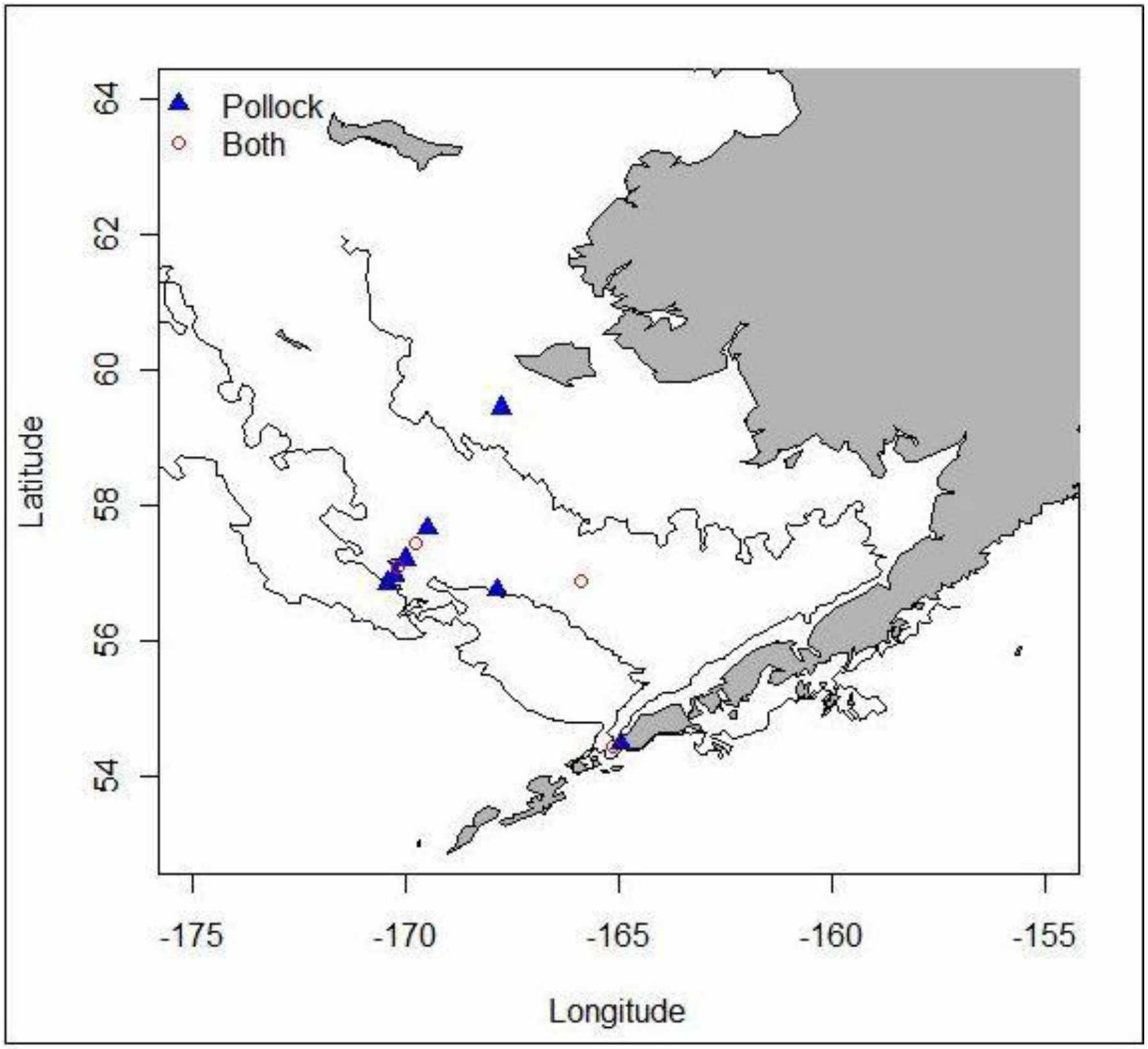

Figure 2. Sampling sites for flexion walleye pollock and Pacific cod larvae from the BEST/BSIERP cooperative in the southeastern Bering Sea in July, 2008.

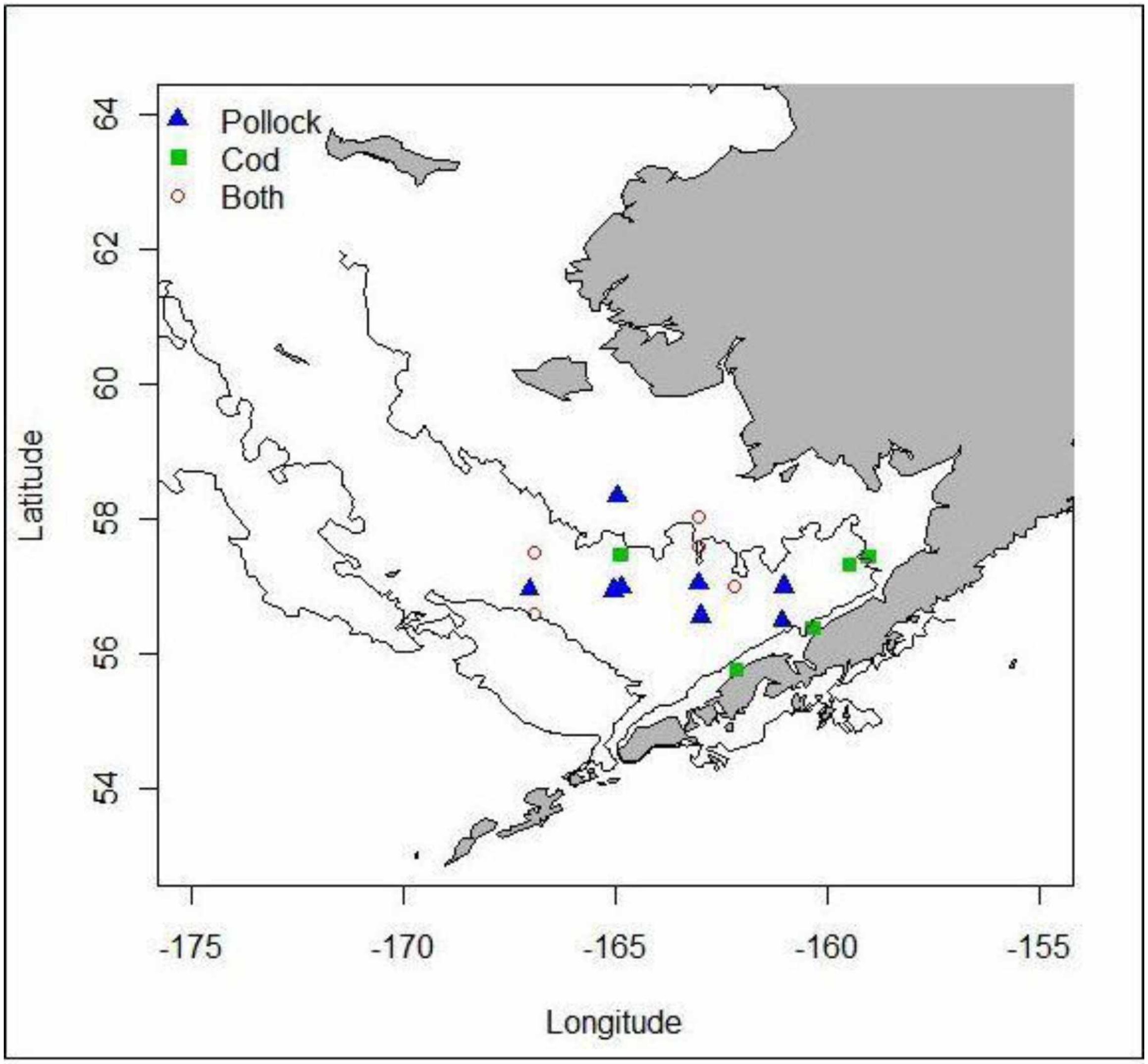

Figure 3. Sampling sites for juvenile walleye pollock and Pacific cod from the BASIS (TSMRI)/FOCI (AFSC) cruises in the southeastern Bering Sea in September, 2008.

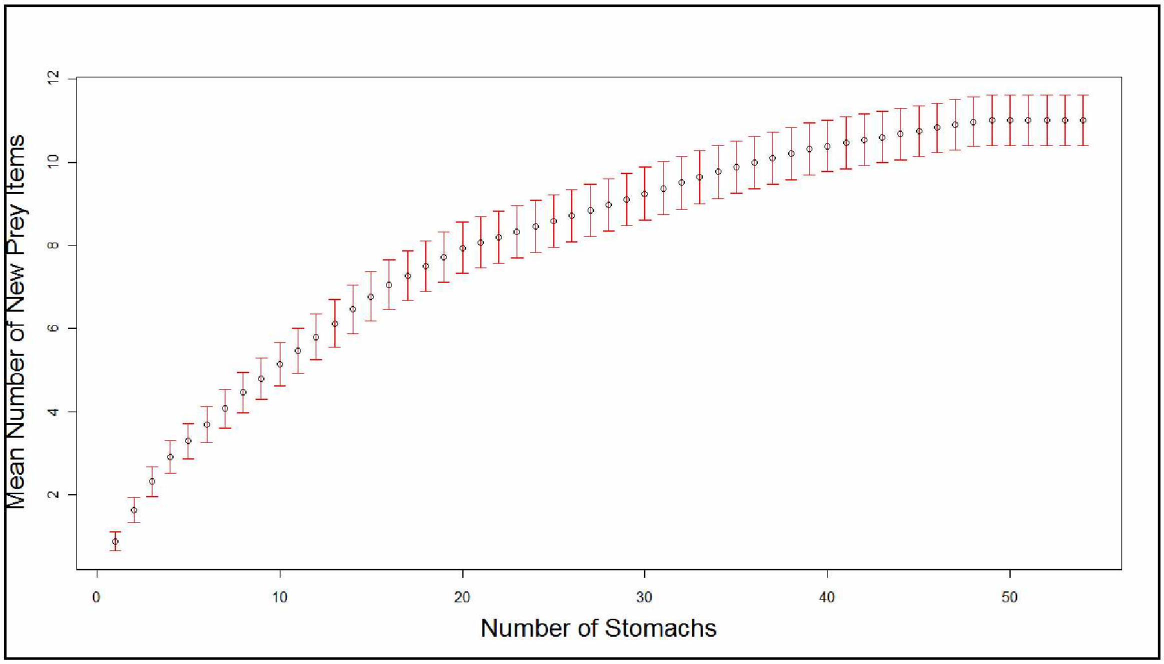

Figure 4. Cumulative prey curve for spring walleye pollock, error bars represent 95% confidence intervals. If the curve reaches an asymptote the number of stomachs processed is sufficient to describe dietary breadth.

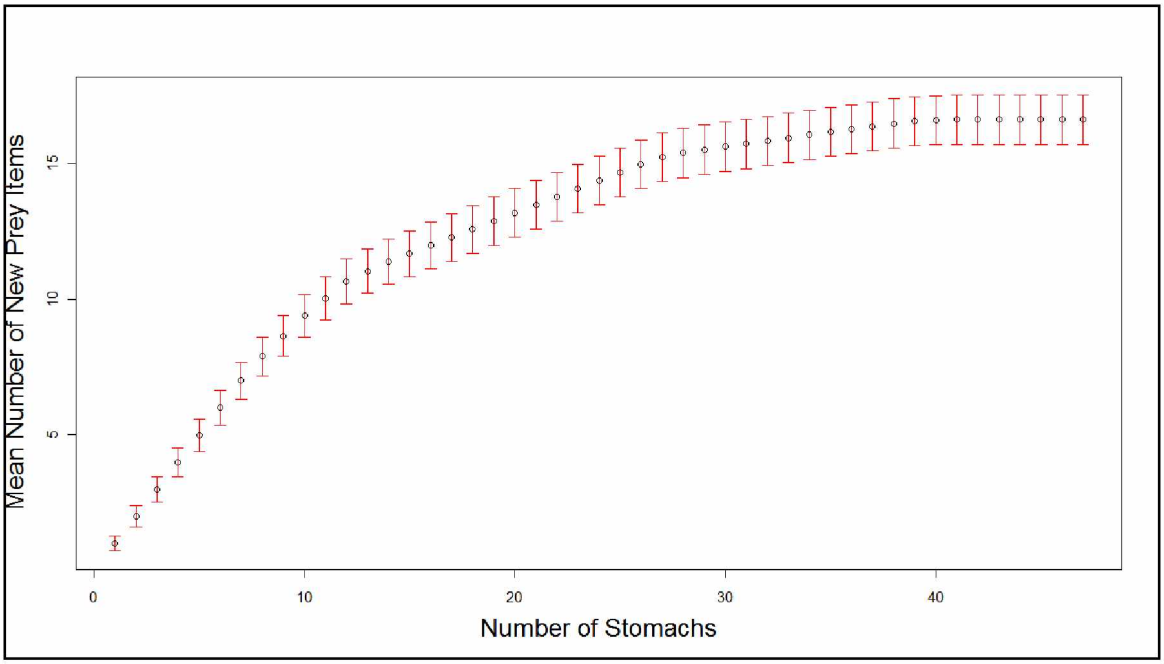

Figure 5. Cumulative prey curve for spring Pacific cod, error bars represent 95% confidence intervals. If the curve reaches an asymptote the number of stomachs processed is sufficient to describe dietary breadth.

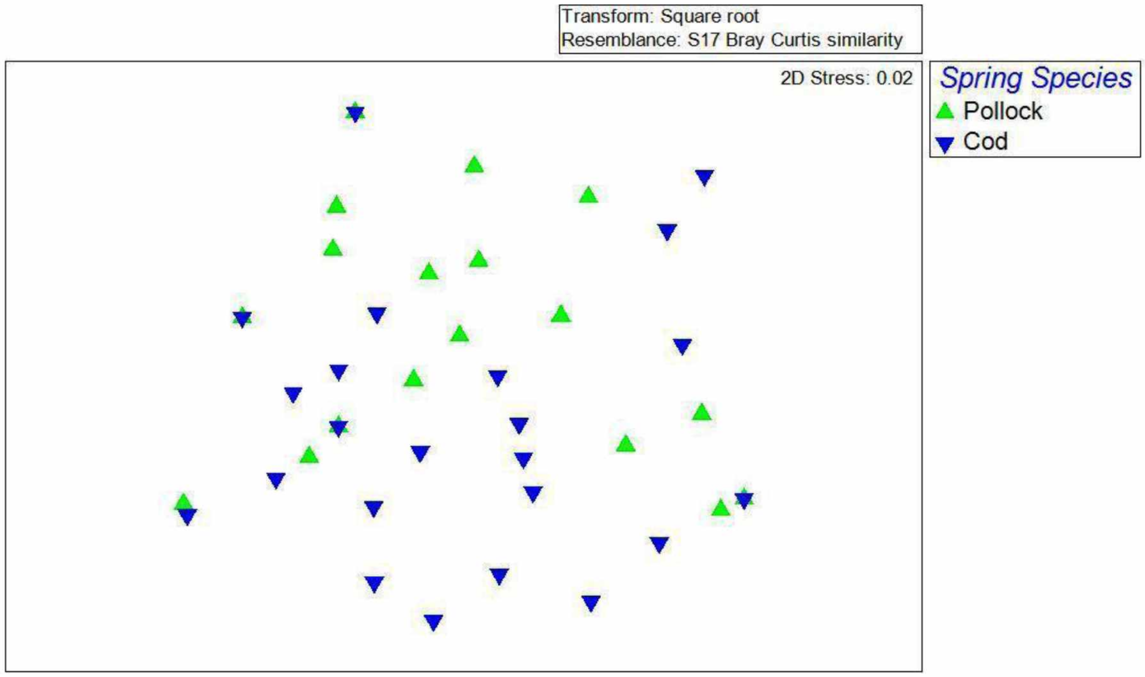

Figure 6. Non-metric multidimensional scaling (NMDS) ordination based on Bray-Curtis similarity matrix depicting the dietary composition of spring walleye pollock and Pacific cod larvae in the southeastern Bering Sea. Data were square-root transformed. 2D stress represents how well the plot can be represented in two dimensions (PRIMER: Kruskal stress formula 1).

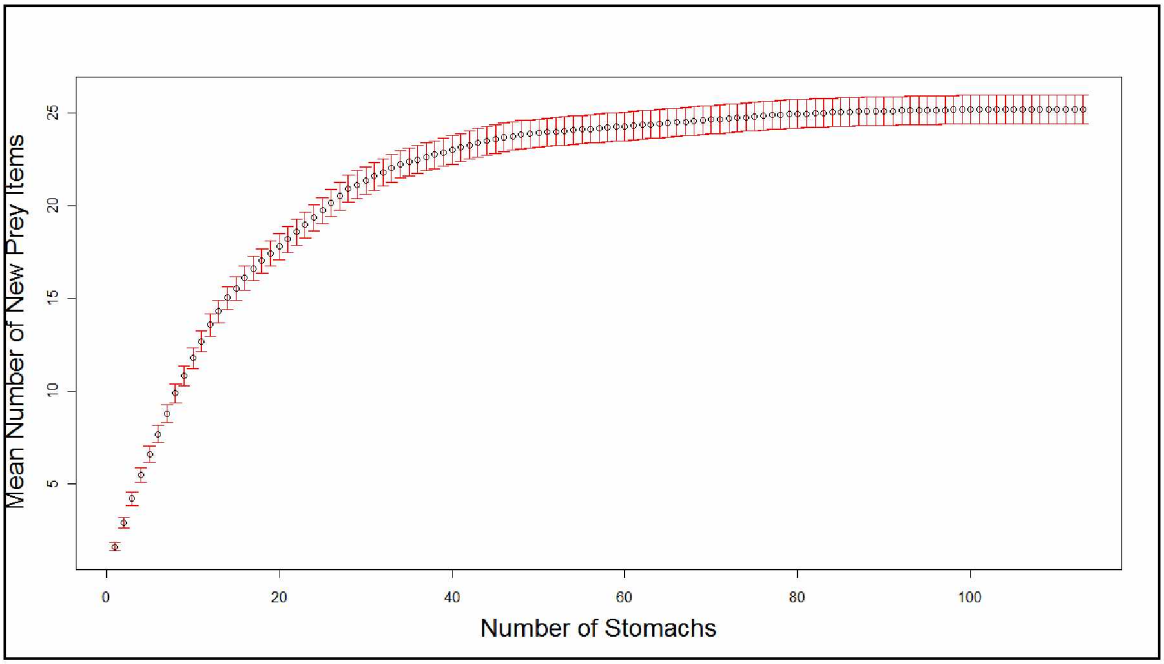

Figure 7. Cumulative prey curve for summer walleye pollock, error bars represent 95% confidence intervals. If the curve reaches an asymptote the number of stomachs processed is sufficient to describe dietary breadth.

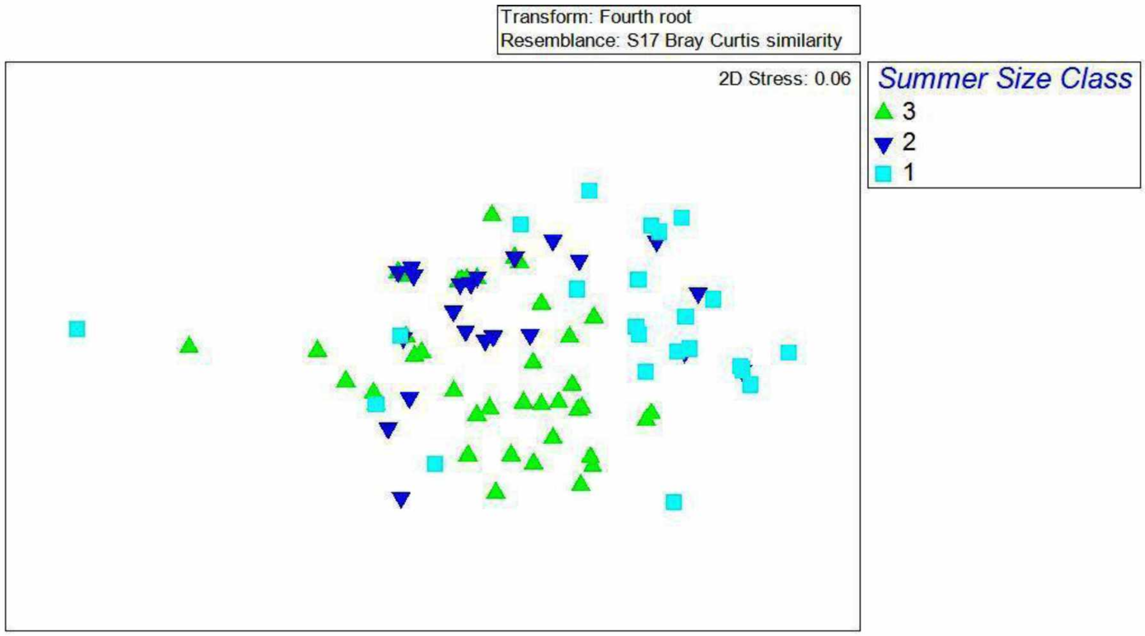

Figure 8. Non-metric multidimensional scaling (NMDS) ordination based on Bray-Curtis similarity matrix depicting the dietary composition of summer walleye pollock larvae in the southeastern Bering Sea by size class. Data were fourth-root transformed. 2D stress represents how well the plot can be represented in two dimensions (PRIMER: Kruskal stress formula 1).

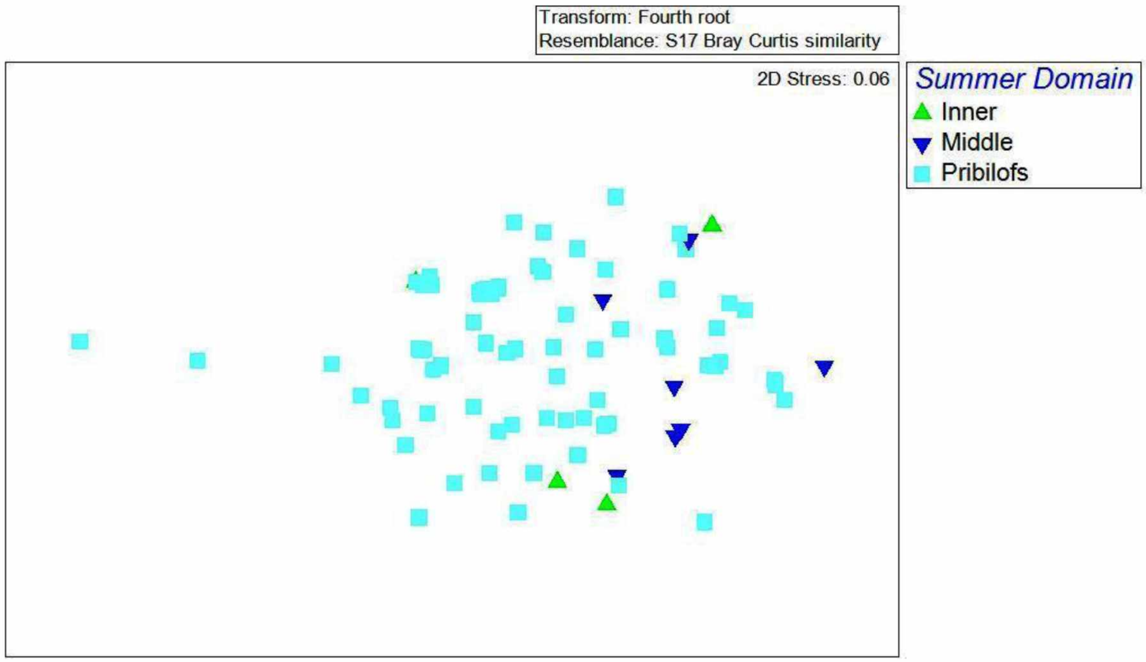

Figure 9. Non-metric multidimensional scaling (NMDS) ordination based on Bray-Curtis similarity matrix depicting the dietary composition of summer walleye pollock larvae in the southeastern Bering Sea by domain. Data were fourth-root transformed. 2D stress represents how well the plot can be represented in two dimensions (PRIMER: Kruskal stress formula 1).

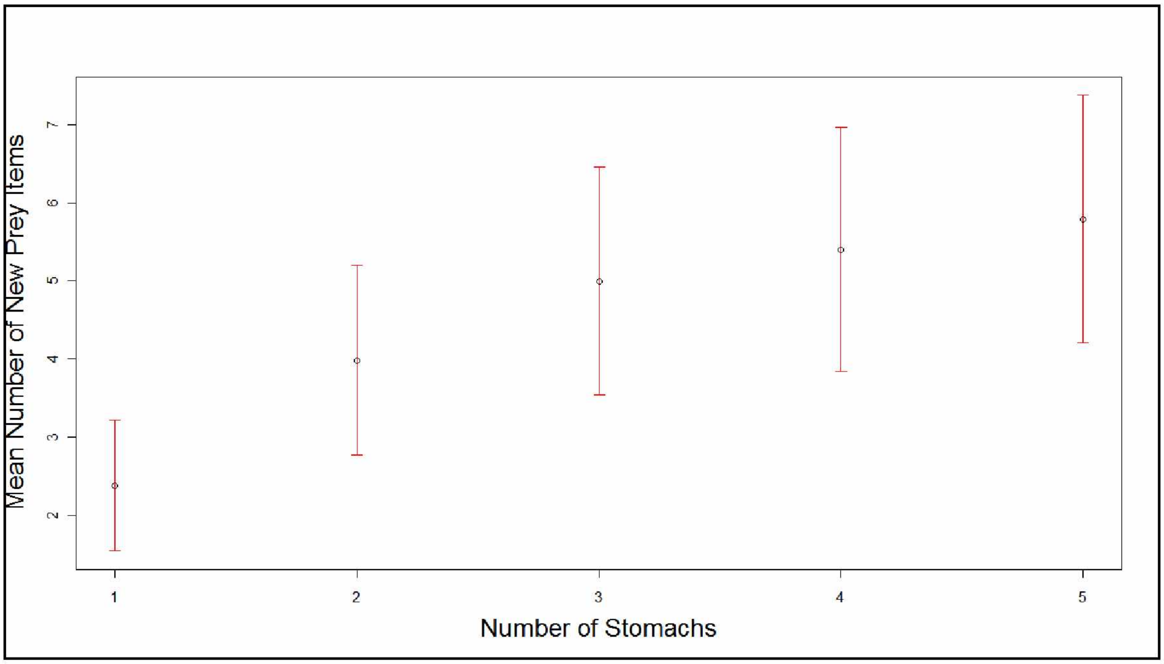

Figure 10. Cumulative prey curve for summer Pacific cod, error bars represent 95% confidence intervals. If the curve reaches an asymptote the number of stomachs processed is sufficient to describe dietary breadth.

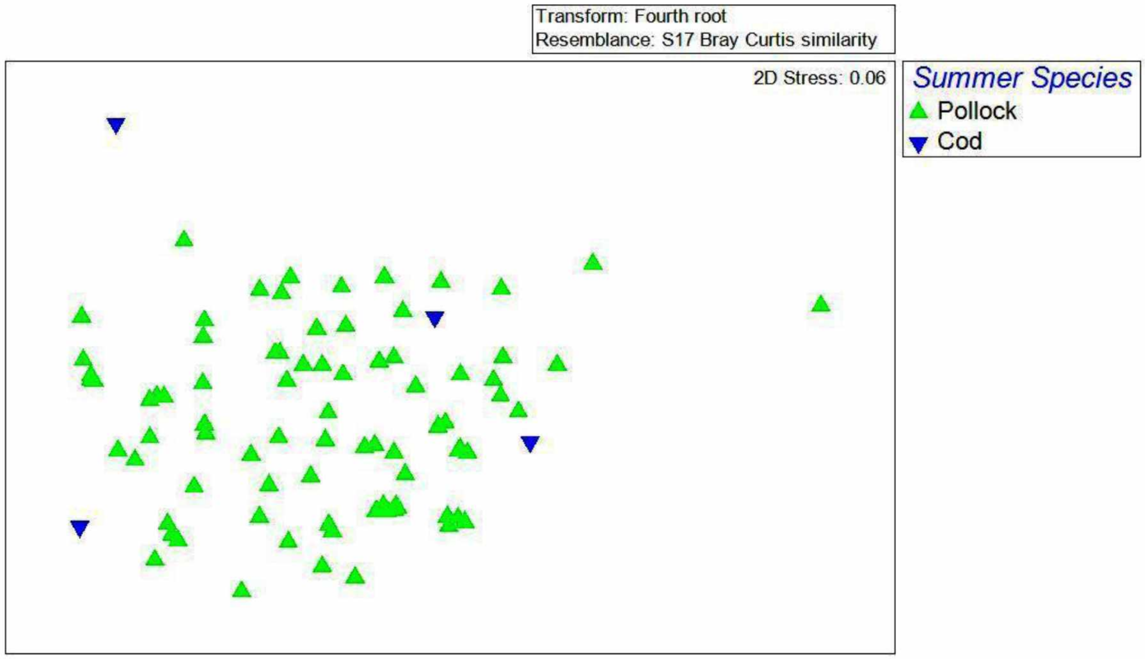

Figure 11. Non-metric multidimensional scaling (NMDS) ordination based on Bray-Curtis similarity matrix depicting the dietary composition of summer walleye pollock and Pacific cod larvae in the southeastern Bering Sea. Data were fourth-root transformed. 2D stress represents how well the plot can be represented in two dimensions (PRIMER: Kruskal stress formula 1).

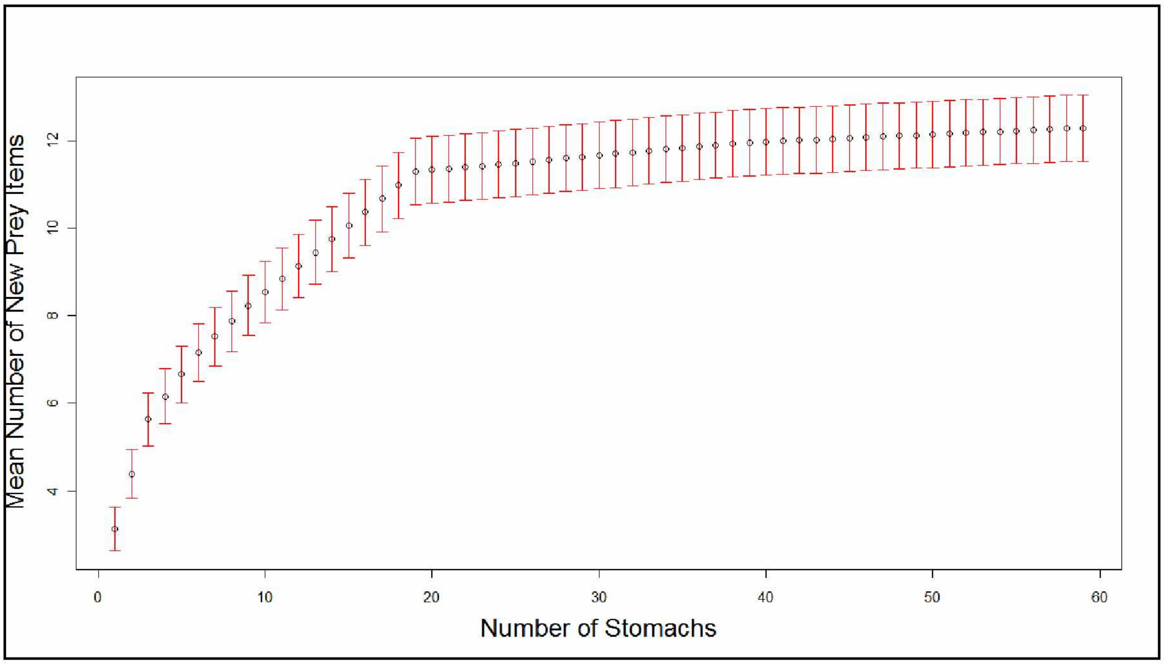

Figure 12. Cumulative prey curve for fall walleye pollock, error bars represent 95% confidence intervals. If the curve reaches an asymptote the number of stomachs processed is sufficient to describe dietary breadth.

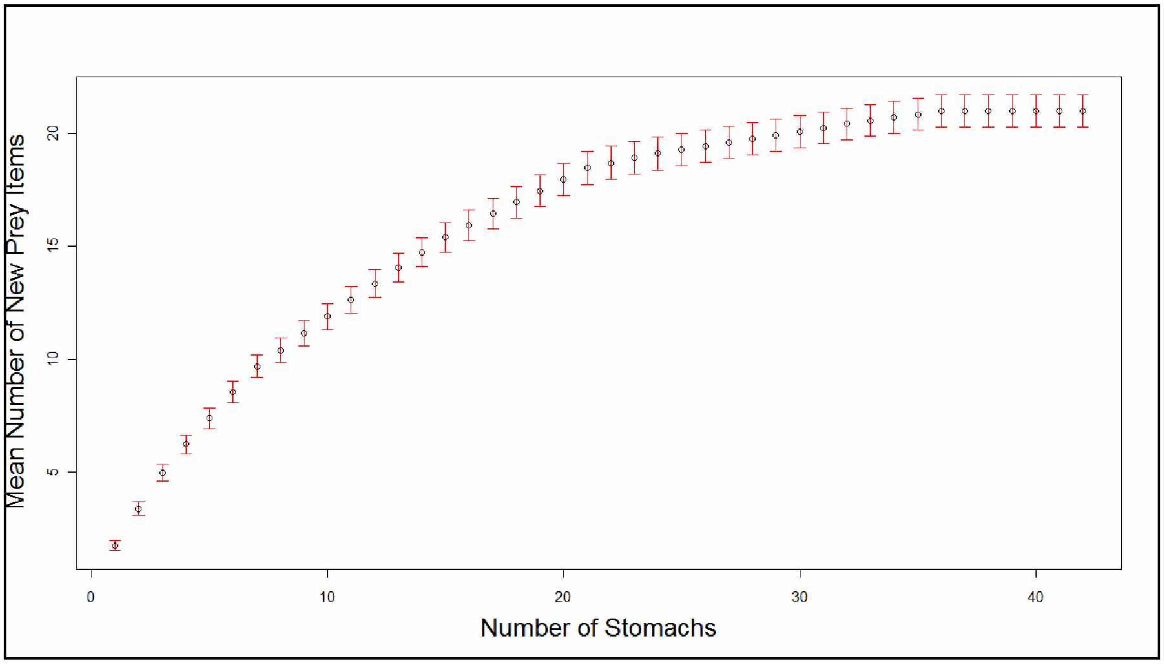

Figure 13. Cumulative prey curve for fall Pacific cod, error bars represent 95% confidence intervals. If the curve reaches an asymptote the number of stomachs processed is sufficient to describe dietary breadth.

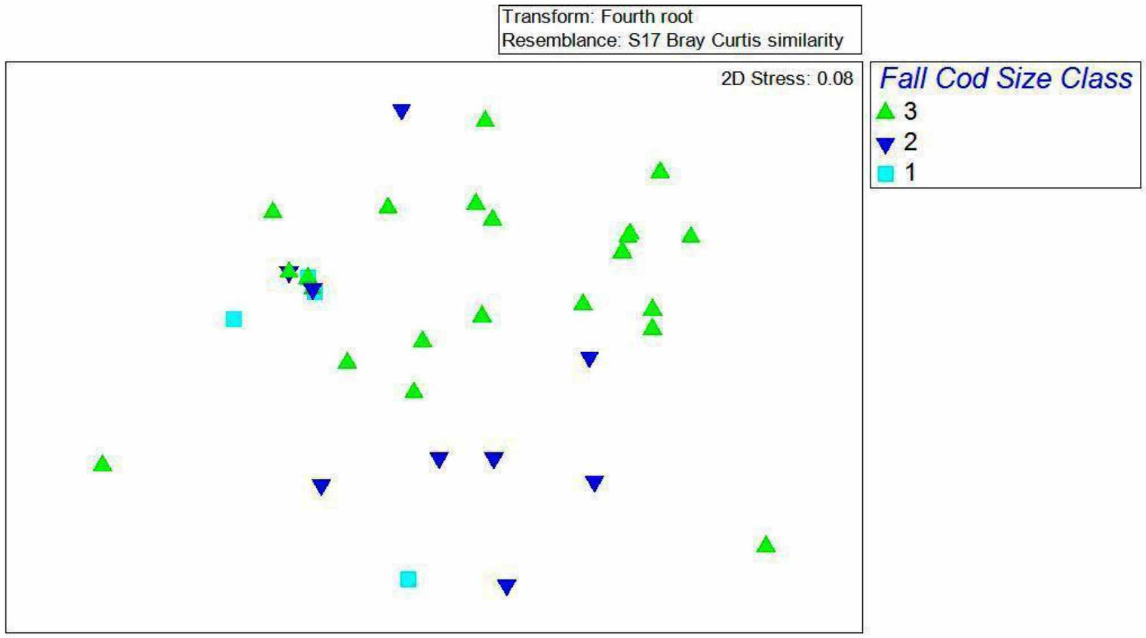

Figure 14. Non-metric multidimensional scaling (NMDS) ordination based on Bray-Curtis similarity matrix depicting the dietary composition of fall Pacific cod juveniles in the southeastern Bering Sea by size class. Data were fourth-root transformed. 2D stress represents how well the plot can be represented in two dimensions (PRIMER: Kruskal stress formula 1).

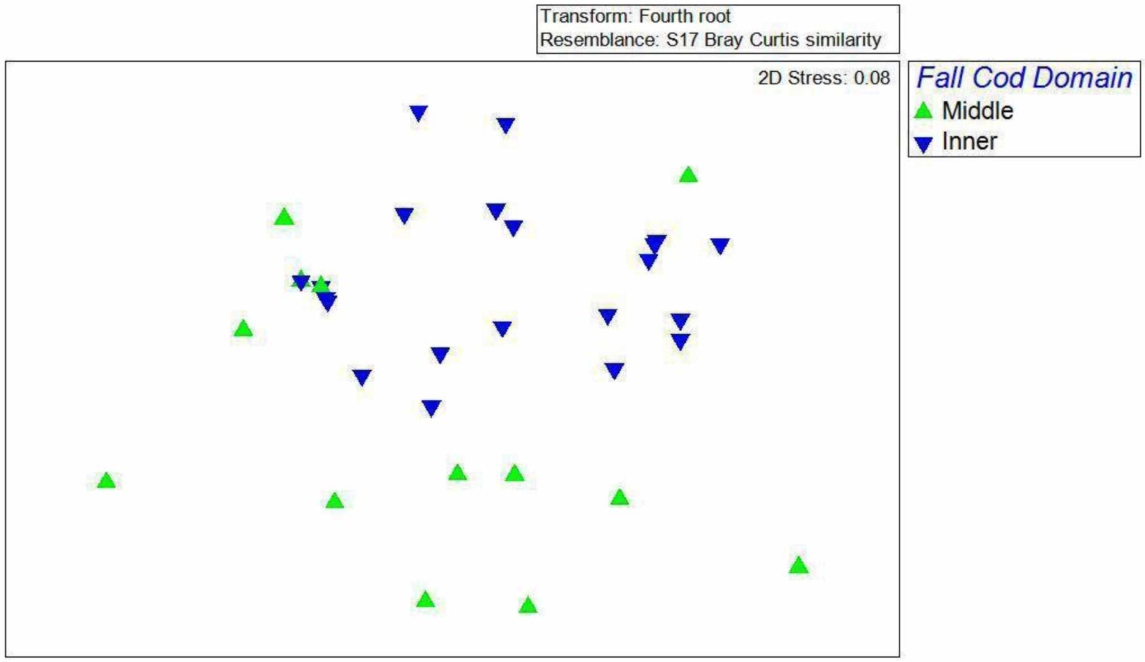

Figure 15. Non-metric multidimensional scaling (NMDS) ordination based on Bray-Curtis similarity matrix depicting the dietary composition of fall Pacific cod juveniles in the southeastern Bering Sea by domain. Data were fourth-root transformed. The ordination represents a subset excluding outer domain diet points, all outer domain diets consisted almost exclusively of Chionoecetes spp. megalope and stretched the ordination out and lumped all Middle and Inner Domain samples into an indistinguishable cluster. 2D stress represents how well the plot can be represented in two dimensions (PRIMER: Kruskal stress formula 1).

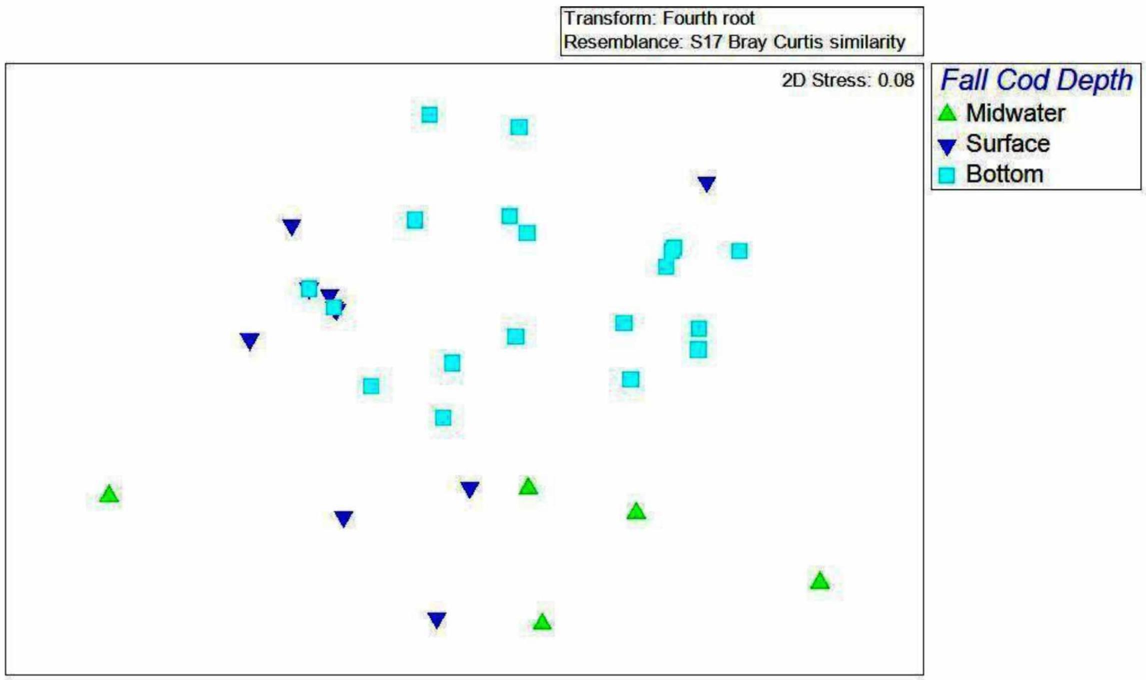

Figure 16. Non-metric multidimensional scaling (NMDS) ordination based on Bray-Curtis similarity matrix depicting the dietary composition of fall Pacific cod juveniles in the southeastern Bering Sea by depth layer. Data were fourth-root transformed. 2D stress represents how well the plot can be represented in two dimensions (PRIMER: Kruskal stress formula 1).

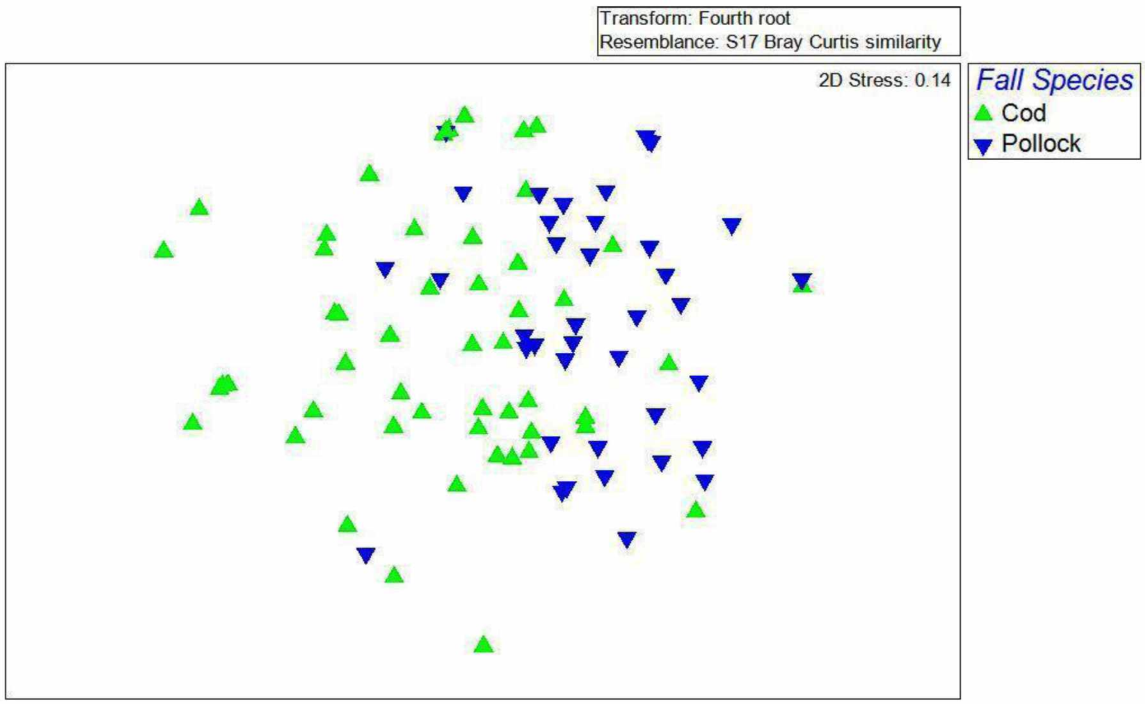

Figure 17. Non-metric multidimensional scaling (NMDS) ordination based on Bray-Curtis similarity matrix depicting the dietary composition of fall walleye pollock and Pacific cod juveniles in the southeastern Bering Sea. Data were fourth-root transformed. 2D stress represents how well the plot can be represented in two dimensions (PRIMER: Kruskal stress formula 1).

Table 1. Sample size (*n*) of walleye pollock and Pacific cod received in 2008 by season (spring, summer, and fall), agency or project, sample gear, and mesh size. NOAA AFSC=National Oceanic and Atmospheric Administration – Alaska Fisheries Science Center, SFOS BEST/BSIERP=School of Fisheries and Ocean Sciences Bering Ecosystem Studies-Bering Sea Integrated Ecosystem Research Project, TSMRI= Ted Stephens Marine Research Institute.

Season	Project/Agency	Gear	Mesh size	Walleye Pollock *n*	Pacific cod *n*
Spring	NOAA AFSC	Bongo	335µm	54	47
Summer	SFOS BEST/BSIERP	MOCNESS	500µm	113	5
Fall	NOAA TSMRI	Rope Trawl	1.2cm	62	22
Fall	NOAA AFSC	Beam Trawl	7mm	-	20

Table 2. Sample stratification by size class, domain, and depth distribution within each season (*n* = sample size for each variable). Each size class is the result of the 33rd and 66th percentile of the length frequency distribution and is represented as a range of standard length (SL) for spring and summer and a range of fork length (FL) for the fall season. NA: not available; capture depth presented in meters except for fall trawl sampling.

		Spring		Summer		Fall	
		Pollock	Cod	Pollock	Cod	Pollock	Cod
Size Class [mm]	**1**	3.2-5.6 n=21	3.0-5.1 n=17	4.4-10.1 n=39	NA	36.2-66.7 n=27	52.8-64.4 n=9
	2	5.7-6.1 n=17	5.2-5.9 n=15	10.2-12.5 n=27	9.1-16.4 n=5	66.8-70.4 n=7	64.5-69.6 n=9
	3	6.2-7.4 n=16	6.0-7.6 n=15	12.6-22 n=47	NA	70.5-88 n=28	69.7-87.2 n=24
Domain	**Inner**	n=8	n=11	n=8	n=1	n=10	n=23
	Middle	n=24	n=14	n=10	n=1	n=46	n=13
	Outer	n=22	n=22	n=95	n=3	n=6	n=6
Capture Depth [m]	**20-0**	NA	NA	n=89	n=3	surface n=42	surface n=11
	40-20	NA	NA	n=20	n=1	midwater n=20	midwater n=11
	60-40	NA	NA	n=4	n=1	NA	bottom n=20

Table 3. T-tests for significant differences in mean estimated prey volume, fullness index score, and prey per stomach by size class and domain for spring walleye pollock larvae collected in the southeastern Bering Sea May, 2008. The t-statistic (t_{df}) with its associated degrees of freedom and P-value are shown. Bold values indicate significant differences.

Spring walleye pollock	**mean prey volume**	**mean fullness**	**mean prey*per stomach**
size class tests			
1 vs. 2	$\boldsymbol{t_{24} = -2.5; P \leq 0.01}$	$\boldsymbol{t_{31} = -2.0; P \leq 0.05}$	$t_{13} = 0.8; P > 0.05$
1 vs. 3	$t_{20} = 0.1; P > 0.05$	$t_{30} = -1.0; P > 0.05$	$t_{14} = 1.5; P > 0.05$
2 vs. 3	$\boldsymbol{t_{30} = 2.8; P \leq 0.01}$	$t_{29} = 1.5; P > 0.05$	$t_{19} = 1.5; P > 0.05$
Domain Tests			
Inner vs. Middle	$t_{29} = -0.2; P > 0.05$	$t_{26} = 1.2; P > 0.05$	$t_{14} = 1.7; P > 0.05$
Inner vs. Outer	$t_{30} = -1.5; P > 0.05$	$t_{25} = 0.4; P > 0.05$	$t_{13} = 1.3; P > 0.05$
Middle vs. Outer	$t_{31} = -1.3; P > 0.05$	$t_{39} = -0.7; P > 0.05$	$t_{19} = -0.6; P > 0.05$

Table 4. Diet composition by size class of walleye pollock pre-flexion larvae as percent number (%N), percent volume (%V), percent frequency of occurrence (%FO), and percent index of relative importance (%IRI). "*n*" represents the sample size of all actively feeding larvae, excluding yolk-sac larvae, empty stomachs, and samples with no identifiable prey items. NI-VI: naupliar stages, CI-IV: copepodite stages.

Spring Pollock	**Size Class 1 (*n*=5)**				**Size Class 2 (*n*=10)**				**Size Class 3 (*n*=11)**			
Prey Items	**%N**	**%V**	**%FO**	**%IRI**	**%N**	**%V**	**%FO**	**%IRI**	**%N**	**%V**	**%FO**	**%IRI**
Copepod Eggs	7.7	29.6	20.0	11.9	0.0	0.0	0.0	0.0	21.4	41.5	18.2	31.4
Calanus marshallae NVI	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Eucalanus spp. NIII	0.0	0.0	0.0	0.0	11.1	10.9	20.0	8.1	0.0	0.0	0.0	0.0
Metridia pacifica NII-III	30.8	10.4	20.0	13.1	11.1	1.4	20.0	4.6	7.1	1.2	0.9	0.2
Metridia pacifica NIV-VI	7.7	29.6	20.0	11.9	33.3	46.5	30.0	44.2	0.0	0.0	0.0	0.0
Oithona similis NV-VI	0.0	0.0	0.0	0.0	5.6	3.3	10.0	1.6	7.1	5.8	9.1	3.2
Pseudocalanus spp. NII-III	46.2	10.3	60.0	54.1	5.6	0.4	10.0	1.1	28.6	3.2	36.4	31.8
Pseudocalanus spp. NIV-VI	0.0	0.0	0.0	0.0	22.2	27.0	40.0	36.4	7.1	12.1	9.1	4.8
Calanus marshallae CI-II	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Metridia pacifica CIII	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Microcalanus spp. CIV	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	7.1	8.0	9.1	3.8
Barnacle Cyprids	0.0	0.0	0.0	0.0	11.1	10.5	10.0	4.0	0.0	0.0	0.0	0.0
Diatoms	7.7	20.1	20.0	8.9	0.0	0.0	0.0	0.0	21.4	28.2	18.2	24.8
Euphausiid Calyptopis	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0

Table 5. PRIMER ANOSIM and PERMDISP test results for comparing pollock and cod spring diets. ANOSIM results are presented as the Global R statistic (G.R) across all test groups and the resulting P Value (P). PERMDISP results are presented as the Global F statistic (G.F) across all test groups, associated degrees of freedom (df1,2), Pairwise t statistic (P.t), and resulting P value (P). Bold values indicate significant differences.

	ANOSIM		**PERMDISP**			
Spring Pollock	**G.R**	**P**	**G.F**	**df1**	**df2**	**P**
Size Class	0.05	>0.05	0.50	2	24	>0.05
Domain	-0.03	>0.05	3.37	2	24	>0.05
Spring Cod	**G.R**	**P**	**G.F**	**df1**	**df2**	**P**
Size Class	-0.03	>0.05	5.79	2	21	>0.05
Domain	0.02	>0.05	0.73	2	21	>0.05
Spring Species	**G.R**	**P**	**G.F**	**df1**	**df2**	**P**
pollock vs. cod	0.04	**≤0.05**	2.07	1	49	>0.05

Table 6. Diet composition by domain of walleye pollock pre-flexion larvae as percent number (%N), percent volume (%V), percent frequency of occurrence (%FO), and percent index of relative importance (%IRI). "*n*" represents the sample size of all actively feeding larvae, excluding yolk-sac larvae, empty stomachs, and samples with no identifiable prey items. NI-VI: naupliar stages, CI-IV: copepodite stages.

Spring Pollock	**Inner Domain (*n*=5)**				**Middle Domain (*n*=11)**				**Outer Domain (*n*=10)**			
Prey Items	**%N**	**%V**	**%FO**	**%IRI**	**%N**	**%V**	**%FO**	**%IRI**	**%N**	**%V**	**%FO**	**%IRI**
Copepod Eggs	0.0	0.0	0.0	0.0	6.3	11.7	9.1	4.7	17.6	23.6	20.0	16.7
Calanus marshallae NVI	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Eucalanus spp. NIII	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	11.8	11.0	20.0	9.2
Metridia pacifica NII-III	40.0	10.1	60.0	41.8	6.3	1.0	9.1	1.9	0.0	0.0	0.0	0.0
Metridia pacifica NIV-VI	6.7	19.3	20.0	7.2	18.8	35	9.1	14.2	35.3	47.1	30.0	50.2
Oithona similis NV-VI	0.0	0.0	0.0	0.0	6.3	4.9	9.1	2.9	5.9	3.3	10.0	1.9
Pseudocalanus spp. NII-III	20.0	3.4	20.0	6.5	31.3	3.4	36.4	36.5	17.6	1.4	30.0	11.6
Pseudocalanus spp. NIV-VI	6.7	16.8	20.0	6.5	12.5	20.3	18.2	17.3	11.8	13.7	20.0	10.3
Calanus marshallae CI-II	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Metridia pacifica CIII	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Microcalanus spp. CIV	6.7	11.1	20.0	5.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Barnacle Cyprids	0.0	0.0	0.0	0.0	12.6	15.9	18.2	14.9	0.0	0.0	0.0	0.0
Diatoms	20.0	39.3	40.0	33.0	6.3	7.8	9.1	7.7	0.0	0.0	0.0	0.0
Euphausiid Calyptopis	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0

Table 7. T-tests for significant differences in mean estimated prey volume, fullness index score, and prey per stomach by size class and domain for spring Pacific cod larvae collected in the southeastern Bering Sea May, 2008. T_{df} = t value and associated degrees of freedom, P=corresponding P-value. Bold values indicate significant differences.

Spring Pacific cod	**mean prey volume**	**mean fullness**	**mean prey*per stomach**
size class tests			
1 vs. 2	$t_{18} = 0.9$; $P > 0.05$	$t_{22} = -1.6$; $P > 0.05$	$t_{10} = -0.8$; $P > 0.05$
1 vs. 3	$t_{31} = -0.7$; $P > 0.05$	$\boldsymbol{t_{22} = -3.2; P \leq 0.05}$	$\boldsymbol{t_{13} = -2.6; P \leq 0.05}$
2 vs. 3	$\boldsymbol{t_{43} = -2.5; P \leq 0.01}$	$\boldsymbol{t_{28} = -2.7; P \leq 0.01}$	$\boldsymbol{t_{19} = -2.0; P \leq 0.05}$
Domain Tests			
Inner vs. Middle	$t_{18} = 0.4$; $P > 0.05$	$\boldsymbol{t_{15} = 2.4; P \leq 0.05}$	$t_{8} = 0.6$; $P > 0.05$
Inner vs. Outer	$t_{45} = -1.1$; $P > 0.05$	$t_{30} = 0.7$; $P > 0.05$	$t_{20} = -0.4$; $P > 0.05$
Middle vs. Outer	$t_{31} = -0.9$; $P > 0.05$	$t_{27} = -1.2$; $P > 0.05$	$t_{14} = -1.3$; $P > 0.05$

Table 8. Diet composition by size class of Pacific cod pre-flexion larvae as percent number (%N), percent volume (%V), percent frequency of occurrence (%FO), and percent index of relative importance (%IRI). "*n*" represents the sample size of all actively feeding larvae, excluding yolk-sac larvae, empty stomachs, and samples with no identifiable prey items. NI-VI: naupliar stages, CI-IV: copepodite stages.

Spring Cod	**Size Class 1 (*n=3*)**				**Size Class 2 (*n=9*)**				**Size Class 3 (*n=12*)**			
Prey Items	**%N**	**%V**	**%FO**	**%IRI**	**%N**	**%V**	**%FO**	**%IRI**	**%N**	**%V**	**%FO**	**%IRI**
Copepod Eggs	50.0	13.0	66.7	47.9	25.0	30.1	33.3	26.7	6.9	1.7	16.7	2.4
Calanus marshallae NVI	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	3.4	2.1	8.3	0.8
Eucalanus spp. NIII	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Metridia pacifica NII-III	0.0	0.0	0.0	0.0	6.3	0.7	11.1	1.1	6.9	0.1	8.3	1.0
Metridia pacifica NIV-VI	0.0	0.0	0.0	0.0	31.3	37.6	44.4	44.5	31.0	7.6	58.3	37.4
Oithona similis NV-VI	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Pseudocalanus spp. NII-III	0.0	0.0	0.0	0.0	6.3	0.4	11.1	1.1	10.3	0.1	25.0	4.3
Pseudocalanus spp. NIV-VI	25.0	5.7	33.3	11.7	25.0	26.2	33.3	24.8	0.0	0.0	0.0	0.0
Calanus marshallae CI-II	25.0	81.3	33.3	40.4	0.0	0.0	0.0	0.0	20.7	63.5	33.3	46.5
Metridia pacifica CIII	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	3.4	20.1	8.3	3.2
Microcalanus spp. CIV	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Barnacle Cyprids	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Diatoms	0.0	0.0	0.0	0.0	6.3	5.1	11.1	1.8	10.3	1.7	8.3	1.7
Euphausiid Calyptopis	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	6.9	2.9	16.7	2.7

Table 9. Domain diet composition of Pacific cod pre-flexion larvae as percent number (%N), percent volume (%V), percent frequency of occurrence (%FO), and percent index of relative importance (%IRI). "*n*" represents the sample size of all actively feeding larvae, excluding yolk-sac larvae, empty stomachs, and samples with no identifiable prey items. NI-VI: naupliar stages, CI-IV: copepodite stages.

Spring Cod	Inner Domain (*n=8*)				Middle Domain (*n=2*)				Outer Domain (*n=14*)			
Prey Items	**%N**	**%V**	**%FO**	**%IRI**	**%N**	**%V**	**%FO**	**%IRI**	**%N**	**%V**	**%FO**	**%IRI**
Copepod Eggs	18.8	7.8	25.0	11.3	33.3	36.4	50.0	34.9	13.3	3.8	28.6	9.9
Calanus marshallae NVI	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	3.3	2.4	7.1	0.8
Eucalanus spp. NIII	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Metridia pacifica NII-III	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	10.0	0.2	14.3	3.0
Metridia pacifica NIV-VI	31.3	13.1	50.0	37.8	0.0	0.0	0.0	0.0	30.0	8.5	50.0	38.9
Oithona similis NV-VI	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Pseudocalanus spp. NII-III	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	13.3	0.2	28.6	7.8
Pseudocalanus spp. NIV-VI	6.3	2.3	12.5	1.8	66.7	63.6	50.0	65.1	6.7	1.7	14.3	2.4
Calanus marshallae CI-II	12.5	65.2	25.0	33.1	0.0	0.0	0.0	0.0	16.7	59.1	21.4	32.8
Metridia pacifica CIII	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	3.3	22.4	7.1	3.7
Microcalanus spp. CIV	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Barnacle Cyprids	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Diatoms	25.0	7.1	25.0	13.7	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Euphausiid Calyptopis	6.3	4.5	12.5	2.3	0.0	0.0	0.0	0.0	3.3	1.6	7.1	0.7

Table 10. Feeding intensity of age-0 walleye pollock and Pacific cod expressed as mean prey volume/size, visual fullness index scores, and numerical feeding intensity (±*SD*) for all seasons with corresponding t-statistics, degrees of freedom (*df*) and P-values (*P*). Bold values indicate significant differences.

Spring	**Walleye pollock**	**Pacific cod**	***t***	***df***	***p***
Prey Volume [ml]	0.3 (±0.1)	0.5 (±0.3)	-3.6	57	≤ **0.001**
Fullness (1-6)	2.7 (±1.2)	3.3 (±1.4)	-2.2	85	≤ **0.05**
Prey*Per stomach	1.8 (±1.5)	2.0 (±0.8)	-0.7	49	> 0.05
Summer					
Prey Size [mm]	0.9 (±0.5)	1.7 (±1.7)	-2.1	19	≤ **0.05**
Fullness (1-6)	3.4 (±1.2)	4.4 (±2.2)	-1.6	116	> 0.05
Prey*Per stomach	6.5 (±5.3)	5.0 (±4.1)	0.6	92	> 0.05
Fall					
Prey Size [mm]	2.1 (±2.5)	5.3 (±3.7)	-18.6	525	≤ **0.001**
Fullness (1-6)	3.9 (±1.0)	4.3 (±1.3)	-2.1	99	≤ **0.05**
Prey*Per stomach	74.7 (±98.4)	11.4 (±16.9)	4.1	99	≤ **0.001**

Table 11. Diet composition of walleye pollock and Pacific cod pre-flexion larvae as percent number (%N), percent volume (%V), percent frequency of occurrence (%FO), and percent index of relative importance (%IRI). "*n*" represents the sample size of all actively feeding larvae, excluding yolk-sac larvae, empty stomachs, and samples with no identifiable prey. N I-VI: naupliar stages, C I-VI: copepodite stages.

	Spring Pollock (*n*=26)				**Spring Cod (*n*=24)**			
Prey Items	**%N**	**%V**	**%FO**	**%IRI**	**%N**	**%V**	**%FO**	**%IRI**
Copepod Eggs	10.2	18.2	3.7	3.3	16.3	5.5	29.2	13.9
Calanus marshallae NVI	0.0	0.0	0.0	0.0	2.0	1.7	4.2	0.3
Eucalanus spp. NIII	4.1	5.1	7.4	2.2	0.0	0.0	0.0	0.0
Metridia pacifica NII-III	14.3	2.2	14.8	7.8	6.1	0.2	8.3	1.2
Metridia pacifica NIV-VI	20.4	36.4	18.5	33.3	28.6	9.6	45.8	38.3
Oithona similis NV-VI	4.1	3.1	7.4	1.7	0.0	0.0	0.0	0.0
Pseudocalanus spp. NII-III	22.4	2.3	29.6	23.3	8.2	0.2	16.7	3.0
Pseudocalanus spp. NIV-VI	10.2	15.9	18.5	15.3	10.2	3.0	16.7	4.8
Calanus marshallae CI-II	0.0	0.0	0.0	0.0	14.3	59.6	20.8	33.7
Metridia pacifica CIII	0.0	0.0	0.0	0.0	2.0	16.1	4.2	1.7
Microcalanus spp. CIV	2.0	2.1	3.7	0.5	0.0	0.0	0.0	0.0
Barnacle Cyprids	4.1	4.8	1.9	4.1	0.0	0.0	0.0	0.0
Diatoms	8.2	9.9	5.6	8.5	8.2	1.7	4.2	1.7
Euphausiid Calyptopis	0.0	0.0	0.0	0.0	4.1	2.3	8.3	1.2

Table 12. T-tests for significant differences in mean estimated prey size, fullness index score, and prey per stomach by size class, domain, and depth for summer walleye pollock larvae collected in the southeastern Bering Sea July, 2008. T_{df}=t value and corresponding degrees of freedom, P=corresponding P-value. Bold values indicate significant differences.

Summer walleye pollock	mean prey size	mean fullness	mean prey per stomach
size class tests			
1 vs. 2	**t_{271}=-11.5; $P \leq$ 0.001**	t_{64} = -1.2; P > 0.05	**t_{47} =-2.3; $P \leq$ 0.05**
1 vs. 3	**t_{426} =-12.2; $P \leq$0.001**	t_{84} =-1.5; P > 0.05	**t_{66} =-2.6; $P \leq$ 0.01**
2 vs. 3	**t_{473} = -2.1; $P \leq$ 0.05**	t_{72} = -0.2; P > 0.05	t_{61} =-0.3; P > 0.05
Domain Tests			
Inner vs. Middle	**t_{73} = 7.0; $P \leq$ 0.001**	t_{16} =-1.0; P > 0.05	t_{11} =-0.5; P > 0.05
Inner vs. Pribilofs	t_{535} = 0.6; P > 0.05	**t_{101} = -1.7; $P \leq$0.05**	t_{79} =-0.7; P > 0.05
Middle vs. Pribilofs	**t_{562} = -8.0; $P \leq$0.001**	t_{103} = -0.5; P > 0.05	t_{82} =-0.1; P > 0.05
Depth Tests			
0-20 vs. 20-40	**t_{572}=-11.7; $P \leq$ 0.001**	**t_{107} =-2.4; $P \leq$ 0.01**	t_{85} =-0.3; P > 0.05
0-20 vs. 40-60	**t_{468} =-3.4; $P \leq$ 0.001**	t_{91} = 0.5; P > 0.05	t_{70} = 0.0; P > 0.05
20-40 vs. 40-60	t_{140} = 1.5; P > 0.05	**t_{22} = 2.0; $P \leq$ 0.05**	t_{19} = 0.1; P > 0.05

Table 13. Diet composition by size class of walleye pollock flexion larvae as percent number (%N), percent volume (%V), percent frequency of occurrence (%FO), and percent index of relative importance (%IRI). "*n*" represents the sample size of all actively feeding larvae, excluding empty stomachs and samples with no identifiable prey items. NII-VI: naupliar stages, CII-VI: copepodite stages.

Summer Pollock	**Size Class 1 (*n=27*)**				**Size Class 2 (*n=22*)**				**Size Class 3 (*n=41*)**			
Prey Items	**%N**	**%W**	**%FO**	**%IRI**	**%N**	**%W**	**%FO**	**%IRI**	**%N**	**%W**	**%FO**	**%IRI**
Acartia spp. NIII	0.9	0.4	3.7	0.1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Neocalanus spp. NII	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1.0	0.1	2.4	<0.1
Pseudocalanus spp. NIV-VI	82.0	37.4	66.7	90.8	21.3	1.9	27.3	7.8	4.1	0.2	12.2	0.8
Acartia longiremis CIV-VI	0.9	3.7	3.7	0.2	30.0	24.0	54.5	36.3	19.4	8.9	51.2	21.1
Calanus marshallae CIII	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	2.5	9.7	4.9	0.9
Calanus marshallae CIV-VI	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1.0	17.5	7.3	2.0
Centropages abdominalis CII	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Centropages abdominalis CV	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Metridia pacifica CIII-IV	1.8	4.9	3.7	0.3	0.0	0.0	0.0	0.0	2.2	0.7	2.4	0.1
Neocalanus spp. CII-IV	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.6	16.7	2.4	0.6
Neocalanus cristatus CV	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Oithona similis CII-VI	5.3	6.4	14.8	2.0	0.0	0.0	0.0	0.0	21.3	2.8	43.9	15.4
Pseudocalanus spp. CII-III	4.4	9.3	11.1	1.7	25.0	10.1	54.5	23.6	16.2	3.8	26.8	7.8
Pseudocalanus spp. CIV-VI	2.7	29.7	11.1	4.1	20.0	43.1	36.4	28.3	30.8	38.1	51.2	51.3
Other Copepodites	0.0	0.0	0.0	0.0	3.1	20.4	13.6	4.0	0.3	1.2	2.4	0.1
Themisto pacifica	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Other	1.8	8.3	7.4	0.8	0.6	0.6	4.6	0.1	0.6	0.3	4.9	0.1

Table 14. PRIMER ANOSIM and PERMDISP test results for comparing diets of summer pollock and cod. ANOSIM results are presented as the Global R statistic (G.R) across all test groups, Pairwise R (P.R) for specific group tests, and the resulting P Value (P). PERMDISP results are presented as the Global F statistic (G.F) across all test groups, associated degrees of freedom (df1,2), Pairwise t statistic (P.t), and resulting P value (P). Bold values indicate significant differences.

	ANOSIM			**PERMDISP**				
Summer Pollock	**G.R**	**P.R**	**P**	**G.F**	**df1**	**df2**	**P.t**	**P**
Size Class	0.20	-	**≤0.001**	2.32	2	87	-	>0.05
1 vs. 2	-	0.17	**≤0.001**	-	-	-	-	-
1 vs. 3	-	0.27	**≤0.01**	-	-	-	-	-
2 vs. 3	-	0.12	**≤0.05**	-	-	-	-	-
Domain	0.07	-	**≤0.05**	3.05	2	87	-	>0.05
Inner vs. Middle	-	0.05	>0.05	-	-	-	-	-
Inner vs. Pribilofs	-	0.11	**≤0.05**	-	-	-	-	-
Middle vs. Pribilofs	-	0.05	>0.05	-	-	-	-	-
Depth	0.04	-	>0.05	9.00	2	87	-	>0.05
Summer Species	**G.R**	**P.R**	**P**	**G.F**	**df1**	**df2**	**P.t**	**P**
pollock vs. cod	0.14	-	**≤0.05**	0.63	1	92	-	>0.05

Table 15. Diet composition by domain of walleye pollock flexion larvae as percent number (%N), percent volume (%V), percent frequency of occurrence (%FO), and percent index of relative importance (%IRI). "*n*" represents the sample size of all actively feeding larvae, excluding empty stomachs and samples with no identifiable prey items. NII-VI: naupliar stages, CII-VI: copepodite stages.

Summer Pollock	**Inner Domain** (*n=5*)				**Middle Domain** (*n=8*)				**Pribilofs** (*n=77*)			
Prey Items	**%N**	**%W**	**%FO**	**%IRI**	**%N**	**%W**	**%FO**	**%IRI**	**%N**	**%W**	**%FO**	**%IRI**
Acartia spp. NIII	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.2	<0.1	1.3	<0.1
Neocalanus spp. NII	0.0	0.0	0.0	0.0	5.9	2.8	12.5	0.8	0.0	0.0	0.0	0.0
Pseudocalanus spp. NIV-VI	8.3	0.3	20.0	2.1	31.4	14.9	75.0	25.4	23.8	1.6	28.6	12.8
Acartia longiremis CIV-VI	8.3	2.9	40.0	5.5	0.0	0.0	0.0	0.0	21.1	13.0	41.6	25.0
Calanus marshallae CIII	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1.6	8.0	2.6	0.4
Calanus marshallae CIV-VI	4.2	57.1	20.0	15.1	0.0	0.0	0.0	0.0	0.4	9.7	2.6	0.5
Centropages abdominalis CII	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Centropages abdominalis CV	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Metridia pacifica CIII-IV	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1.8	0.7	2.6	0.1
Neocalanus spp. CII-IV	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.4	13.8	1.3	0.3
Neocalanus cristatus CV	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Oithona similis CII-VI	38.0	3.7	80.0	40.5	58.8	73.8	75.0	72.7	6.6	1.2	16.9	2.3
Pseudocalanus spp. CII-III	0.0	0.0	0.0	0.0	3.9	8.6	12.5	1.1	18.3	5.7	32.5	13.8
Pseudocalanus spp. CIV-VI	38.0	34.5	40.0	35.4	0.0	0.0	0.0	0.0	24.0	39.9	39.0	43.9
Other Copepodites	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1.2	5.9	5.2	0.7
Themisto pacifica	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Other	4.2	1.6	20.0	1.4	0.0	0.0	0.0	0.0	0.8	0.5	5.2	0.1

Table 16. Diet composition by depth strata of walleye pollock flexion larvae as percent number (%N), percent volume (%V), percent frequency of occurrence (%FO), and percent index of relative importance (%IRI). "*n*" represents the sample size of all actively feeding larvae, excluding empty stomachs and samples with no identifiable prey items. NII-VI: naupliar stages, CII-VI: copepodite stages.

Summer Pollock	**20-0m** (*n=70*)				**40-20m** (*n=18*)				**60-40m** (*n=3*)			
Prey Items	**%N**	**%W**	**%FO**	**%IRI**	**%N**	**%W**	**%FO**	**%IRI**	**%N**	**%W**	**%FO**	**%IRI**
Acartia spp. NIII	0.2	<0.1	1.5	<0.1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Neocalanus spp. NII	0.7	0.1	1.5	<0.1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Pseudocalanus spp. NIV-VI	31.0	3.2	43.5	29.2	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Acartia longiremis CIV-VI	20.0	18.6	33.3	24.8	16.3	5.4	50.0	11.6	10.5	2.9	66.7	8.0
Calanus marshallae CIII	1.8	14.0	2.9	0.9	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Calanus marshallae CIV-VI	0.4	16.9	2.9	1.0	0.0	0.0	0.0	0.0	5.3	58.7	33.3	19.0
Centropages abdominalis CII	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Centropages abdominalis CV	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Metridia pacifica CIII-IV	2.0	1.3	2.9	0.2	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Neocalanus spp. CII-IV	0.0	0.0	0.0	0.0	1.6	30.9	5.6	1.9	0.0	0.0	0.0	0.0
Neocalanus cristatus CV	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Oithona similis CII-VI	13.0	3.6	24.6	8.0	5.7	0.6	16.7	1.1	36.8	3.0	66.7	23.7
Pseudocalanus spp. CII-III	18.0	8.5	29.0	14.7	13.8	2.3	33.3	5.8	0.0	0.0	0.0	0.0
Pseudocalanus spp. CIV-VI	12.0	29.6	26.1	20.9	57.7	51.5	66.7	77.9	47.4	35.4	66.7	49.3
Other Copepodites	0.4	3.4	2.9	0.2	3.3	8.8	11.1	1.4	0.0	0.0	0.0	0.0
Themisto pacifica	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Other	0.7	0.7	4.4	0.1	1.6	0.6	11.1	0.3	0.0	0.0	0.0	0.0

Table 17. Diet composition of walleye pollock and Pacific cod flexion larvae as percent number (%N), percent volume (%V), percent frequency of occurrence (%FO), and percent index of relative importance (%IRI). "*n*" represents the sample size of all actively feeding larvae, excluding empty stomachs and samples with no identifiable prey. NII-VI: naupliar stages, CII-VI: copepodite stages.

	Summer Pollock (*n=91*)				**Summer Cod (*n=4*)**			
Prey Items	**%N**	**%W**	**%FO**	**%IRI**	**%N**	**%W**	**%FO**	**%IRI**
Acartia spp. NIII	0.2	<0.1	1.1	<0.1	0.0	0.0	0.0	0.0
Neocalanus spp. NII	0.5	<0.1	1.1	<0.1	5.0	<0.1	25.0	2.2
Pseudocalanus spp. NIV-VI	23.8	1.7	32.2	15.6	5.0	<0.1	25.0	2.2
Acartia longiremis CIV-VI	18.7	12.1	37.8	22.1	0.0	0.0	0.0	0.0
*Calanus marshall*ae CIII	1.4	7.3	2.2	0.4	20.0	3.7	25.0	10.2
Calanus marshallae CIV-VI	0.5	13.2	3.3	0.9	0.0	0.0	0.0	0.0
Centropages abdominalis CII	0.0	0.0	0.0	0.0	15.0	0.8	25.0	6.8
Centropages abdominalis CV	0.0	0.0	0.0	0.0	15.0	1.6	25.0	7.1
Metridia pacifica CIII-IV	1.5	0.7	2.2	0.1	0.0	0.0	0.0	0.0
Neocalanus spp. CII-IV	0.3	12.6	1.1	0.3	0.0	0.0	0.0	0.0
Neocalanus cristatus CV	0.0	0.0	0.0	0.0	5.0	74.9	25.0	34.5
Oithona similis CII-VI	12.4	2.3	24.4	6.8	0.0	0.0	0.0	0.0
Pseudocalanus spp. CII-III	16.3	5.3	28.9	11.9	0.0	0.0	0.0	0.0
Pseudocalanus spp. CIV-VI	22.5	38.9	35.6	41.4	30.0	1.8	50.0	27.4
Other Copepodites	1.0	5.4	4.4	0.5	0.0	0.0	0.0	0.0
Themisto pacifica	0.0	0.0	0.0	0.0	5.0	17.2	25.0	9.6
Other	0.9	0.6	5.6	0.2	0.0	0.0	0.0	0.0

Table 18. T-tests for significant differences in mean estimated prey size, fullness index score, and prey per stomach by size class, domain, and depth for fall walleye pollock juveniles collected in the southeastern Bering Sea September, 2008. T_{df}=t value and associated degrees of freedom, *P*=corresponding P-value. Bold values indicate significant differences.

Fall walleye pollock	mean prey size	mean fullness	mean prey*per stomach
size class tests			
1 vs. 2	**t_{2271}=-5.3; $P \leq 0.001$**	$t_{29} = 0.3$; $P > 0.05$	$t_{29} = 1.0$; $P > 0.05$
1 vs. 3	**t_{3221}=-8.4; $P \leq 0.001$**	$t_{50} = 0.6$; $P > 0.05$	$t_{47} = 1.5$; $P > 0.05$
2 vs. 3	$t_{1660} = -0.8$; $P > 0.05$	$t_{33} = 0.2$; $P > 0.05$	t_{30} =-0.1; $P > 0.05$
Domain Tests			
Inner vs. Middle	**$t_{3632} = 8.3$; $P \leq 0.001$**	**$t_{52} = 2.1$; $P \leq 0.05$**	$t_{52} = 0.1$; $P > 0.05$
Inner vs. Outer	t_{889}=-0.5; $P > 0.05$	**$t_{13} = 3.7$; $P \leq 0.01$**	**$t_{13} = 2.9$; $P > 0.05$**
Middle vs. Outer	**$t_{2825} = -3.2$; $P \leq 0.001$**	$t_{47} = 1.3$; $P > 0.05$	$t_{47} = 1.5$; $P > 0.05$
Depth Test			
Surface vs. Midwater	**t_{4405}=-5.9; $P \leq 0.001$**	t_{57} =-0.7; $P > 0.05$	t_{57}=-0.5; $P > 0.05$

Table 19. Diet composition by size class of walleye pollock juveniles as percent number (%N), percent volume (%V), percent frequency of occurrence (%FO), and percent index of relative importance (%IRI). "*n*" represents the sample size of all actively feeding larvae, excluding empty stomachs and samples with no identifiable prey items. CIV-VI: copepodite stages.

Fall Pollock	**Size Class 1 (*n*=22)**				**Size Class 2 (*n*=7)**				**Size Class 3 (*n*=25)**			
Prey Items	**%N**	**%W**	**%FO**	**%IRI**	**%N**	**%W**	**%FO**	**%IRI**	**%N**	**%W**	**%FO**	**%IRI**
Acartia longiremis CV	6.0	3.6	45.8	5.1	1.4	0.6	14.3	0.3	3.3	1.1	17.9	0.8
Acartia longiremis CVI	1.3	0.1	8.3	0.2	0.8	0.1	14.3	0.1	1.2	0.1	7.1	0.1
Calanus marshallae CIV-VI	6.5	18.9	20.8	3.2	12.9	27.0	57.1	21.6	29.3	46.4	60	46.8
Centropages abdominalis CVI	5.0	1.0	8.3	0.6	2.2	0.3	14.3	0.4	0.2	<0.1	7.1	<0.1
Epilabidocera amphitrites CV-VI	0.1	0.1	4.2	0.0	5.1	4.9	57.1	5.4	2.6	1.9	10.7	0.5
Pseudocalanus spp. CV	11.1	1.1	25	3.8	6.2	0.4	28.6	1.8	0.6	<0.1	14.3	0.1
Pseudocalanus spp. CVI	64.7	9.5	58.3	54.5	64.6	6.8	57.1	38.6	57.2	4.6	60.7	38.7
Euphausia pacifica	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.2	0.2	3.6	<0.1
Thysanoessa spp.	1.9	29.3	37.5	9.7	2.3	34.1	85.7	23.9	1.9	28.5	21.4	6.7
Chionoecetes spp. Megalopae	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Themisto pacifica	0.1	0.5	4.2	0.0	0.0	0.0	0.0	0.0	0.5	2.8	21.4	0.7
Limacina helicina	0.1	<0.1	4.2	0.0	0.6	<0.1	14.3	0.1	0.1	0.0	3.6	<0.1
Parasagitta elegans	3.1	35.6	45.8	22.8	3.1	25.6	28.6	7.8	2.3	14.6	32.1	5.6
Oikopleura spp.	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.1	0.1	3.6	<0.1
Other	0.4	0.1	12.5	0.1	0.8	0.2	14.3	0.1	0.1	<0.1	3.6	<0.1

Table 20. PRIMER ANOSIM and PERMDISP test results for comparing diets of fall pollock and cod across size classes and domains. ANOSIM results are presented as the Global R statistic (G.R) across all test groups, Pairwise R (P.R) for specific group tests, and the resulting P Value (P). PERMDISP results are presented as the Global F statistic (G.F) across all test groups, associated degrees of freedom (df1,2), Pairwise t statistic (P.t), and resulting P value (P). Bold values indicate significant differences.

	ANOSIM			PERMDISP				
Fall Pollock	**G.R**	**P.R**	**P**	**G.F**	**df1**	**df2**	**P.t**	**P**
Size Class	-0.01	-	>0.05	0.705	2	56	-	>0.05
Domain	0.11	-	>0.05	9.94	2	56	-	**≤0.01**
Inner vs. Middle	-	-	-	-	-	-	4.38	**≤0.01**
Inner vs. Outer	-	-	-	-	-	-	0.24	>0.05
Middle vs. Outer	-	-	-	-	-	-	2.72	>0.05
Fall Cod	**G.R**	**P.R**	**P**	**G.F**	**df1**	**df2**	**P.t**	**P**
Size Class	0.17	-	**≤0.01**	0.71	2	39	-	>0.05
1 vs. 2	-	0.21	**≤0.05**	-	-	-	-	-
1 vs. 3	-	0.20	**≤0.01**	-	-	-	-	-
2 vs. 3	-	0.12	**≤0.05**	-	-	-	-	-
Domain	0.34	-	**≤0.001**	64.39	2	39	-	**≤0.001**
Inner vs. Middle	-	0.20	**≤0.01**	-	-	-	2.42	**≤0.05**
Inner vs. Outer	-	0.55	**≤0.001**	-	-	-	8.98	**≤0.001**
Middle vs. Outer	-	0.40	**≤0.001**	-	-	-	14.27	**≤0.001**

Table 21. Diet composition by domain of walleye pollock juveniles as percent number (%N), percent volume (%V), percent frequency of occurrence (%FO), and percent index of relative importance (%IRI). "*n*" represents the sample size of all actively feeding larvae, excluding empty stomachs and samples with no identifiable prey items. CIV-VI: copepodite stages.

Fall Pollock	**Inner Domain (*n=10*)**				**Middle Domain (*n=44*)**				**Outer Domain (*n=5*)**			
Prey Items	**%N**	**%W**	**%FO**	**%IRI**	**%N**	**%W**	**%FO**	**%IRI**	**%N**	**%W**	**%FO**	**%IRI**
Acartia longiremis CV	2.0	0.5	30.0	0.5	4.8	2.4	29.5	2.1	0.0	0.0	0.0	0.0
Acartia longiremis CVI	4.0	0.2	30.0	0.9	0.5	<0.1	4.5	<0.1	0.0	0.0	0.0	0.0
Calanus marshallae CIV-VI	1.1	1.3	30.0	0.5	24.0	56.7	61.4	49.0	92.9	77.0	80.0	95.7
Centropages abdominalis CVI	0.0	0.0	0.0	0.0	3.2	0.5	11.4	0.4	0.0	0.0	0.0	0.0
Epilabidocera amphitrites CV-VI	7.9	4.4	70.0	6.0	<0.1	<0.1	2.3	0.0	0.0	0.0	0.0	0.0
Pseudocalanus spp. CV	0.0	0.0	0.0	0.0	7.2	0.6	27.3	2.1	0.0	0.0	0.0	0.0
Pseudocalanus spp. CVI	73.4	4.5	90.0	48.5	56.4	6.8	59.1	36.5	0.0	0.0	0.0	0.0
Euphausia pacifica	0.4	0.3	10.0	<0.1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Thysanoessa spp.	5.3	59.8	80.0	31.5	1.0	12.4	29.5	2.8	0.0	0.0	0.0	0.0
Chionoecetes spp. Megalopae	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Themisto pacifica	0.0	0.0	0.0	0.0	0.3	2.3	13.6	0.3	2.4	7.3	20.0	1.4
Limacina helicina	0.0	0.0	0.0	0.0	0.1	<0.1	6.8	<0.1	0.0	0.0	0.0	0.0
Parasagitta elegans	6.0	29.0	50.0	12.1	1.8	17.1	36.4	6.7	4.8	15.7	20.0	2.9
Oikopleura spp.	0.0	0.0	0.0	0.0	0.5	<0.1	2.3	<0.1	0.0	0.0	0.0	0.0
Other	0.0	0.0	0.0	0.0	0.3	0.1	11.4	<0.1	0.0	0.0	0.0	0.0

Table 22. Diet composition by depth strata of walleye pollock juveniles as percent number (%N), percent volume (%V), percent frequency of occurrence (%FO), and percent index of relative importance (%IRI). "*n*" represents the sample size of all actively feeding larvae, excluding empty stomachs and samples with no identifiable prey items. CIV-VI: copepodite stages.

Fall Pollock	Surface (*n=41*)				Mid-Water (*n=18*)			
Prey Items	%N	%W	%FO	%IRI	%N	%W	%FO	%IRI
Acartia longiremis CV	5.8	2.6	31.7	2.6	1.1	0.4	16.7	0.3
Acartia longiremis CVI	0.6	<0.1	4.9	<0.1	2.3	0.1	16.7	0.4
Calanus marshallae CIV-VI	27.3	59.1	61.0	51.1	6.6	11.4	50.0	10.1
Centropages abdominalis CVI	3.8	0.6	12.2	0.5	0.0	0.0	0.0	0.0
Epilabidocera amphitrites CV-VI	1.9	1.9	12.2	0.4	0.9	0.7	16.7	0.3
Pseudocalanus spp. CV	3.9	0.3	22.0	0.9	9.4	0.5	16.7	1.8
Pseudocalanus spp. CVI	52.9	5.8	63.4	36.1	71.0	6.2	50.0	43.1
Euphausia pacifica	0.0	0.0	0.0	0.0	0.2	0.2	5.6	<0.1
Thysanoessa spp.	1.4	17.8	36.6	5.2	2.6	41.3	33.3	13.6
Chionoecetes spp. Megalopae	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Themisto pacifica	0.3	2.5	14.6	0.4	0.1	0.4	5.6	<0.1
Limacina helicina	<0.1	<0.1	2.4	<0.1	0.2	<0.1	11.1	<0.1
Parasagitta elegans	1.1	9.2	26.8	2.7	5.6	38.6	61.1	30.2
Oikopleura spp.	0.6	<0.1	2.4	<0.1	0.0	0.0	0.0	0.0
Other	0.4	0.1	12.2	0.1	0.0	0.0	0.0	0.0

Table 23. PRIMER ANOSIM and PERMDISP fall pollock and cod test results (depth interval and species). ANOSIM results are presented as the Global R statistic (G.R) across all test groups, Pairwise R (P.R) for specific group tests, and the resulting P Value (P). PERMDISP results are presented as the Global F statistic (G.F) across all test groups, associated degrees of freedom (df1,2), Pairwise t statistic (P.t), and resulting P value (P). Bold values indicate significant differences.

	ANOSIM			**PERMDISP**				
Fall Pollock	**G.R**	**P.R**	**P**	**G.F**	**df1**	**df2**	**P.t**	**P**
Surface vs Mid-water	0.042	-	>0.05	0.10	1	57	-	>0.05
Fall Cod	**G.R**	**P.R**	**P**	**G.F**	**df1**	**df2**	**P.t**	**P**
Depth Interval	0.31	-	**≤0.001**	0.23	2	39	-	>0.05
Surface vs Mid-water	-	0.34	**≤0.001**	-	-	-	-	-
Surface vs Bottom	-	0.14	**≤0.05**	-	-	-	-	-
Midwater vs Bottom	-	0.44	**≤0.001**	-	-	-	-	-
Species	**G.R**	**P.R**	**P**	**G.F**	**df1**	**df2**	**P.t**	**P**
Pollock vs Cod	0.07	-	**≤0.01**	14.34	1	99	-	**≤0.001**

Table 24. T-tests for significant differences in mean estimated prey size, fullness index score, and prey per stomach by size class, domain, and depth for fall Pacific cod juveniles collected in the southeastern Bering Sea September, 2008. T_{df}=t value and corresponding degrees of freedom, P=corresponding P-value. Bold values indicate significant differences.

Fall Pacific cod	mean prey size	mean fullness	mean prey*per stomach
size class tests			
1 vs. 2	$\boldsymbol{t_{117} = 4.3; P \leq 0.001}$	$t_{16} = 1.6; P > 0.05$	$\boldsymbol{t_{16} = -1.9; P \leq 0.05}$
1 vs. 3	$\boldsymbol{t_{379} = 8.0; P \leq 0.001}$	$t_{31} = 0.5; P > 0.05$	$\boldsymbol{t_{31} = -1.9; P \leq 0.05}$
2 vs. 3	$t_{458} = 1.5; P > 0.05$	$t_{31} = -1.2; P > 0.05$	$t_{31} = -0.6; P > 0.05$
Domain Tests			
Inner vs. Middle	$\boldsymbol{t_{469} = -2.5; P \leq 0.01}$	$t_{34} = 1.5; P > 0.05$	$\boldsymbol{t_{34} = 2.1; P \leq 0.05}$
Inner vs. Outer	$\boldsymbol{t_{410} = -14.2; P > 0.001}$	$t_{27} = -1.0; P > 0.05$	$\boldsymbol{t_{27} = 2.0; P \leq 0.05}$
Middle vs. Outer	$\boldsymbol{t_{71} = -5.9; P \leq 0.001}$	$\boldsymbol{t_{17} = -1.9; P \leq 0.05}$	$t_{17} = 1.2; P > 0.05$
Depth Test			
Surface vs. Midwater	$\boldsymbol{t_{89} = -2.4; P \leq 0.05}$	$t_{20} = 0.1; P > 0.05$	$t_{20} = 1.5; P > 0.05$
Surface vs. Bottom	$\boldsymbol{t_{455} = 4.3; P \leq 0.001}$	$t_{29} = 0.0; P > 0.05$	$\boldsymbol{t_{29} = -2.0; P \leq 0.05}$
Midwater vs. Bottom	$\boldsymbol{t_{410} = 7.3; P \leq 0.001}$	$t_{29} = -0.2; P > 0.05$	$\boldsymbol{t_{29} = -2.7; P \leq 0.01}$

Table 25. Diet composition by size class of Pacific cod juveniles as percent number (%N), percent volume (%V), percent frequency of occurrence (%FO), and percent index of relative importance (%IRI). "*n*" represents the sample size of all actively feeding larvae, excluding empty stomachs and samples with no identifiable prey items. CIV-VI: copepodite stages.

Fall Cod	**Size Class 1 (*n=9*)**				**Size Class 2 (*n=9*)**				**Size Class 3 (*n=24*)**			
Prey Items	**%N**	**%W**	**%FO**	**%IRI**	**%N**	**%W**	**%FO**	**%IRI**	**%N**	**%W**	**%FO**	**%IRI**
Acartia longiremis CV	0.0	0.0	0.0	0.0	1.0	0.1	11.1	0.2	0.0	0.0	0.0	0.0
Acartia longiremis CVI	0.0	0.0	0.0	0.0	3.1	0.1	11.1	0.6	0.0	0.0	0.0	0.0
Calanus marshallae CIV-VI	0.0	0.0	0.0	0.0	20.8	10.1	22.2	12.2	5.0	3.6	16.7	2.1
Centropages abdominalis CVI	5.0	0.1	11.1	0.8	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Epilabidocera amphitrites CV-VI	0.0	0.0	0.0	0.0	5.2	1.2	22.2	2.5	0.6	0.2	4.2	<0.1
Pseudocalanus spp. CV	0.0	0.0	0.0	0.0	1.0	<0.1	11.1	0.2	0.3	<0.1	4.2	<0.1
Pseudocalanus spp. CVI	5.0	<0.1	11.1	0.8	1.0	<0.1	11.1	0.2	0.3	<0.1	4.2	<0.1
Euphausia pacifica	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Thysanoessa spp.	55.0	81.6	33.3	64.6	38.5	37.8	33.3	22.0	46.0	79.6	87.5	80.3
Chionoecetes spp. Megalopae	25.0	15.4	55.6	31.8	0.0	0.0	0.0	0.0	0.3	0.8	4.2	0.1
Themisto pacifica	5.0	2.9	11.1	1.2	12.5	22.5	44.4	27.7	0.8	2.2	8.3	0.4
Limacina helicina	0.0	0.0	0.0	0.0	2.1	<0.1	11.1	0.4	42.1	0.8	20.8	13.0
Parasagitta elegans	0.0	0.0	0.0	0.0	14.6	28.1	44.4	33.8	4.4	12.7	16.7	4.1
Oikopleura spp.	5.0	<0.1	11.1	0.8	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Other	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.3	<0.1	4.2	<0.1

Table 26. Diet composition by domain of Pacific cod juveniles as percent number (%N), percent volume (%V), percent frequency of occurrence (%FO), and percent index of relative importance (%IRI). "*n*" represents the sample size of all actively feeding larvae, excluding empty stomachs and samples with no identifiable prey items. CIV-VI: copepodite stages.

Fall Cod	Inner Domain (*n=23*)				Middle Domain (*n=13*)				Outer Domain(*n=6*)			
Prey Items	**%N**	**%W**	**%FO**	**%IRI**	**%N**	**%W**	**%FO**	**%IRI**	**%N**	**%W**	**%FO**	**%IRI**
Acartia longiremis CV	0.0	0.0	0.0	0.0	1.5	0.1	7.7	0.2	0.0	0.0	0.0	0.0
Acartia longiremis CVI	0.0	0.0	0.0	0.0	4.5	0.1	7.7	0.7	0.0	0.0	0.0	0.0
Calanus marshallae CIV-VI	4.2	2.7	13.0	1.1	31.8	12.6	23.1	19.2	0.0	0.0	0.0	0.0
Centropages abdominalis CVI	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	14.3	0.3	16.7	1.3
Epilabidocera amphitrites CV-VI	0.5	0.1	4.3	<0.1	7.6	1.4	15.4	2.6	0.0	0.0	0.0	0.0
Pseudocalanus spp. CV	0.0	0.0	0.0	0.0	3.0	<0.1	15.4	0.9	0.0	0.0	0.0	0.0
Pseudocalanus spp. CVI	0.0	0.0	0.0	0.0	4.5	0.1	23.1	2.0	0.0	0.0	0.0	0.0
Euphausia pacifica	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Thysanoessa spp.	51.2	81.8	95.7	81.9	10.6	34.5	38.5	25.2	0.0	0.0	0.0	0.0
Chionoecetes spp. Megalopae	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	85.7	99.7	100.0	98.7
Themisto pacifica	2.0	4.7	13.0	1.1	12.1	17.8	30.8	17.3	0.0	0.0	0.0	0.0
Limacina helicina	38.1	0.7	26.1	12.8	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Parasagitta elegans	4.0	10.0	17.4	3.1	21.2	33.3	30.8	31.5	0.0	0.0	0.0	0.0
Oikopleura spp.	0.0	0.0	0.0	0.0	1.5	<0.1	7.7	0.2	0.0	0.0	0.0	0.0
Other	0.0	0.0	0.0	0.0	1.5	0.1	7.7	0.2	0.0	0.0	0.0	0.0

Table 27. Diet composition by depth strata of Pacific cod juveniles as percent number (%N), percent volume (%V), percent frequency of occurrence (%FO), and percent index of relative importance (%IRI). "*n*" represents the sample size of all actively feeding larvae, excluding empty stomachs and samples with no identifiable prey items. CIV-VI: copepodite stages.

Fall Cod	**Surface (*n=11*)**				**Mid-Water (*n=11*)**				**Bottom (*n=20*)**			
Prey Items	**%N**	**%W**	**%FO**	**%IRI**	**%N**	**%W**	**%FO**	**%IRI**	**%N**	**%W**	**%FO**	**%IRI**
Acartia longiremis CV	1.5	0.1	9.1	0.2	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Acartia longiremis CVI	0.0	0.0	0.0	0.0	13.0	0.2	9.1	2.1	0.0	0.0	0.0	0.0
Calanus marshallae CIV-VI	32.3	7.6	27.3	12.6	0.0	0.0	0.0	0.0	4.4	3.4	15.0	1.5
Centropages abdominalis CVI	0.0	0.0	0.0	0.0	4.3	0.1	9.1	0.7	0.0	0.0	0.0	0.0
Epilabidocera amphitrites CV-VI	6.2	0.7	9.1	0.7	4.3	0.8	9.1	0.8	0.5	0.2	5.0	<0.1
Pseudocalanus spp. CV	0.0	0.0	0.0	0.0	8.7	0.1	18.2	2.7	0.0	0.0	0.0	0.0
Pseudocalanus spp. CVI	3.1	<0.1	18.2	0.7	4.3	0.1	9.1	0.7	0.0	0.0	0.0	0.0
Euphausia pacifica	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Thysanoessa spp.	33.8	72.0	72.7	77.0	0.0	0.0	0.0	0.0	49.4	76.6	95.0	76.9
Chionoecetes spp. Megalopae	0.0	0.0	0.0	0.0	26.1	42.8	54.5	64.2	0.0	0.0	0.0	0.0
Themisto pacifica	6.2	5.4	18.2	2.4	17.4	26.9	18.2	13.8	2.1	6.0	15.0	1.6
Limacina helicina	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	39.6	0.9	30.0	15.6
Parasagitta elegans	15.4	14.3	18.2	6.3	17.4	28.8	18.2	14.3	4.1	12.9	20.0	4.4
Oikopleura spp.	1.5	<0.1	9.1	0.2	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Other	0.0	0.0	0.0	0.0	4.3	0.2	9.1	0.7	0.0	0.0	0.0	0.0

Table 28. Diet composition of walleye pollock and Pacific cod juveniles as percent number (%N), percent volume (%V), percent frequency of occurrence (%FO), and percent index of relative importance (%IRI). "*n*" represents the sample size of all actively feeding larvae, excluding empty stomachs and samples with no identifiable prey. CIV-VI: copepodite stages.

	Fall Pollock (*n=59*)				**Fall Cod (*n=42*)**			
Prey Items	**%N**	**%W**	**%FO**	**%IRI**	**%N**	**%W**	**%FO**	**%IRI**
Acartia longiremis CV	4.2	1.7	27.1	1.7	0.2	<0.1	2.4	<0.1
Acartia longiremis CVI	1.1	0.1	8.5	0.1	0.6	<0.1	2.4	<0.1
Calanus marshallae CIV-VI	20.2	40.3	57.6	37.0	8.0	4.6	14.3	3.5
Centropages abdominalis CVI	2.5	0.4	8.5	0.3	0.2	<0.1	2.4	<0.1
Epilabidocera amphitrites CV-VI	1.5	1.4	13.6	0.4	1.5	0.4	7.1	0.3
Pseudocalanus spp. CV	5.8	0.4	20.3	1.3	0.4	<0.1	4.8	<0.1
Pseudocalanus spp. CVI	59.1	5.9	59.3	41.0	0.6	<0.1	7.1	0.1
Euphausia pacifica	0.1	0.1	1.7	<0.1	0.0	0.0	0.0	0.0
Thysanoessa spp.	1.8	27.1	35.6	8.6	44.9	69.9	64.3	74.7
Chionoecetes spp. Megalopae	0.0	0.0	0.0	0.0	1.3	2.9	14.3	1.1
Themisto pacifica	0.2	1.7	11.9	0.2	3.4	7.2	16.7	3.4
Limacina helicina	0.1	<0.1	5.1	<0.1	32.3	0.5	14.3	9.1
Parasagitta elegans	2.6	20.8	37.3	9.3	6.3	14.4	19.0	7.7
Oikopleura spp.	0.4	<0.1	1.7	<0.1	0.2	<0.1	2.4	<0.1
Other	0.3	0.1	8.5	<0.1	0.2	<0.1	2.4	<0.1

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Appendix A. Percent numerical composition (%N) of all prey taxa (excluding empty stomachs and unidentifiable prey items) found in the diet of larval and juvenile walleye pollock and Pacific cod in the southeastern Bering Sea May-September, 2008.

Spring Diet	walleye pollock %N	Pacific cod %N
Copepod eggs	8.2	14.0
Calanoid Nauplii	19.7	14.0
Calanus marshallae NVI	0.0	1.8
Calanus marshallae CI	0.0	5.3
Calanus marshallae CII	0.0	7.0
Eucalanus spp. NIII	3.3	0.0
Metridia pacifica NII	3.3	3.5
Metridia pacifica NIII	8.2	1.8
Metridia pacifica NIV	16.4	3.5
Metridia pacifica NV	0.0	8.8
Metridia pacifica NVI	0.0	12.3
Metridia pacifica CIII	0.0	1.8
Microcalanus spp. CIV	1.6	0.0
Oithona similis NIV	1.6	0.0
Oithona similis NV	1.6	0.0
Pseudocalanus spp. NII	6.6	5.3
Pseudocalanus spp. NIII	11.5	1.8
Pseudocalanus spp. NIV	1.6	1.8
Pseudocalanus spp. NV	4.9	1.8
Pseudocalanus spp. NVI	1.6	5.3
Barnacle cyprids	3.3	0.0
Diatoms	6.6	7.0
Thysanoessa spp. Calyptopis	0.0	3.5

Summary Diet	walleye pollock %N	Pacific cod %N
Acartia spp. NIII	0.2	0.0
Acartia longiremis copepodite	0.2	0.0
Acartia longiremis CIV	11.8	0.0
Acartia longiremis CV	0.9	0.0
Acartia longiremis CVI	4.4	0.0
Barnacle cyprids	0.2	0.0
Calanus marshallae CIII	1.2	16.0
Calanus marshallae CIV	0.2	0.0
Calanus marshallae CVI	0.3	0.0
Centropages abdominalis CII	0.0	12.0
Centropages abdominalis CV	0.0	12.0
Epilabidocera amphitrites CIII	0.3	0.0
Eucalanus spp. NIV	0.3	0.0
Euphausiid Furcilia	0.3	0.0
Themisto pacifica	0.0	4.0
Metridia pacifica CIII	1.1	0.0
Metridia pacifica CIV	0.3	0.0
Neocalanus spp. NII	0.5	4.0
Neocalanus spp. copepodite	0.3	0.0
Neocalanus cristatus CV	0.0	4.0
Oithona similis CIII	0.3	0.0
Oithona similis CV	0.5	0.0
Oithona similis CVI	0.3	0.0
Oithona similis copepodite	10.0	0.0
Pseudocalanus spp. NIV	5.2	0.0
Pseudocalanus spp. NV	9.5	0.0
Pseudocalanus spp. NVI	6.5	4.0
Pseudocalanus spp. CII	1.8	0.0
Pseudocalanus spp. CIII	12.7	0.0
Pseudocalanus spp. CIV	2.7	0.0
Pseudocalanus spp. CV	7.7	4.0
Pseudocalanus spp. CVI	9.2	20.0
Pseudocalanus spp. copepodite	0.3	0.0
Calanoid Copepodite <2mm	4.4	12.0
Calanoid Nauplii	6.5	8.0

Fall Diet	%N walleye pollock	%N Pacific cod
Acartia longiremis CV	4.2	0.2
Acartia longiremis CVI	1.1	0.6
Calanus marshallae CIV	2.3	3.6
Calanus marshallae CV	17.8	3.1
Calanus marshallae CVI	0.1	1.3
Centropages abdominalis CVI	2.5	0.2
Epilabidocera amphitrites CV	1.5	0.4
Epilabidocera amphitrites CVI	0.0	1.1
Pseudocalanus spp. CV	5.8	0.4
Pseudocalanus spp. CVI	59.1	0.6
Barnacle cyprids	0.2	0.2
Chionoecetes spp. Megalopae	0.0	1.3
Euphausia pacifica	0.1	0.0
Thysanoessa spp. Fur.	0.4	10.7
Thysanoessa spp. Juv.	1.4	34.2
Themisto pacifica	0.2	3.4
Oikopleura spp.	0.4	0.2
Limacina helicina	0.1	32.3
Parasagitta elegans	2.6	6.3
Polychaete larvae	0.0	0.0
unidentified ichthyoplankton	0.1	0.0

Appendix B. Feeding intensity of age-0 walleye pollock and Pacific cod expressed as mean prey volume/size, mean visual fullness index scores, and mean numerical feeding intensity (±*SD*) for all categories and seasons.

Spring walleye pollock	**prey volume (ml)**	**fullness**	**prey*per stomach**
size class 1	0.2 (±0.1)	2.2 (±1.3)	2.6 (±3.0)
size class 2	0.3 (±0.1)	3.2 (±1.4)	1.8 (±1.0)
size class 3	0.2 (±0.1)	2.6 (±0.7)	1.3 (±0.5)
Domain			
Inner Domain	0.3 (±0.1)	3.0 (±1.5)	3.0 (±2.8)
Middle Domain	0.3 (±0.1)	2.5 (±0.8)	1.5 (±0.9)
Outer Domain	0.3 (±0.1)	2.8 (±1.5)	1.7 (±1.1)
Summer walleye pollock	**prey size (mm)**		
size class 1	0.5 (±0.3)	3.2 (±1.4)	4.2 (±5.2)
size class 2	0.9 (±0.4)	3.6 (±1.0)	7.3 (±3.9)
size class 3	1.0 (±0.5)	3.6 (±1.2)	7.7 (±5.6)
Domain			
Inner Domain	1.0 (±0.6)	2.8 (±0.9)	4.8 (±4.8)
Middle Domain	0.4 (±0.1)	3.3 (±1.3)	6.4 (±5.7)
Pribilofs	0.9 (±0.5)	3.5 (±1.2)	6.6 (±5.4)
Depth			
0-20 meters	0.8 (±0.4)	3.3 (±1.3)	6.5 (±5.0)
20-40 meters	1.3 (±0.4)	4.1 (±1.0)	6.8 (±6.5)
40-60 meters	1.1 (±0.6)	3.0 (±0.8)	6.3 (±6.1)
Fall walleye pollock	**prey size (mm)**		
size class 1	1.6 (±1.5)	4.0 (±0.9)	89.5 (±111.8)
size class 2	2.2 (±2.7)	3.9 (±0.7)	50.9 (±47.3)
size class 3	2.3 (±3.0)	3.8 (±1.1)	52.2 (±71.4)
Domain			
Inner Domain	2.7 (±3.7)	4.5 (±0.7)	84.9 (±57.6)
Middle Domain	1.9 (±2.4)	3.8 (±1.0)	79.9 (94.8)
Outer Domain	3.1 (±2.9)	3.2 (±0.4)	8.4 (±5.0)
Depth			
surface	2.0 (±1.8)	3.8 (±1.0)	70.8 (±93.9)
mid-water	2.5 (±3.5)	4.0 (±1.0)	83.6 (±110.2)

Spring Pacific cod	prey volume (ml)	fullness	prey*per stomach
size class 1	0.4 (±0.4)	2.3 (±1.2)	1.3 (±0.6)
size class 2	0.3 (±0.1)	3.0 (±0.8)	1.8 (±0.8)
size class 3	0.5 (±0.3)	4.1 (±1.4)	2.4 (±0.7)
Domain			
Inner Domain	0.4 (±0.3)	3.7 (±1.1)	2.0 (±1.1)
Middle Domain	0.3 (±0.2)	2.6 (±0.8)	1.5 (±0.7)
Outer Domain	0.5 (±0.3)	3.3 (±1.6)	2.1 (0.7)
Summer Pacific cod	**prey size (mm)**		
Overall	1.7 (±1.7)	4.4 (±2.2)	5.0 (±4.1)
Fall Pacific cod	**prey size (mm)**		
size class 1	10.8 (±7.3)	4.7 (±0.9)	2.2 (±1.9)
size class 2	5.5 (±4.5)	3.8 (±1.4)	10.7 (±12.9)
size class 3	5.0 (±2.8)	4.4 (±1.3)	15.0 (±20.0)
Domain			
Inner Domain	5.0 (±2.5)	4.5 (±1.2)	17.6 (±20.1)
Middle Domain	6.0 (±5.6)	3.8 (±1.5)	5.1 (±7.8)
Outer Domain	19.5 (±7.8)	5.0 (±0.0)	1.2 (±0.4)
Depth			
surface	6.5 (±4.7)	4.4 (±1.7)	5.9 (±8.4)
mid-water	10.0 (±9.2)	4.3 (±1.1)	2.1 (±1.5)
bottom	4.9 (±2.5)	4.4 (±1.3)	19.5 (±21.0)

GENERAL CONCLUSION

Spring dietary patterns of walleye pollock and Pacific cod revealed notable differences between co-occurring larval stages of both species. In the spring, although there was not a significant difference in mean numerical feeding intensity, larval Pacific cod were scored higher on the visual fullness index and were ingesting prey with a significantly larger mean volume than walleye pollock larvae. The dietary composition was also significantly different; mainly due to the abundance of late stage *M. pacifica* nauplii in the diet of larval Pacific cod, as well as other, comparatively larger prey types, such as euphausiid calyptopis. In contrast, larval walleye pollock were consuming a higher number of earlier stage *M. pacifica* and *Pseudocalanus* spp. nauplii. Although there was some degree of overlap, the overall composition of the diet was disparate enough to be significantly different.

Dietary composition was considerably different between flexion walleye pollock and Pacific cod on the summer season. While larval Pacific cod were ingesting prey with a larger mean size than walleye pollock larvae, no significant differences were found in mean numerical feeding intensity or fullness. Dietary composition was also significantly different, most notably due to the presence of late developmental stages of the large copepod *N. cristatus* in the larval cod diet, as well as other large prey types such as the hyperiid amphipod *T. pacifica*. In contrast, walleye pollock flexion larvae continued to consume higher numbers of comparatively smaller prey items, such as *Pseudocalanus* spp. and *A. longiremis* copepodites. While the number of Pacific cod larvae available for this study was low, the differences in dietary patterns between the two species were still notable enough to be statistically significant, suggesting a difference in resource use despite an overlap in spatial and temporal distribution.

Differences in feeding patterns between walleye pollock and Pacific cod were most apparent in the fall. Mean prey size and fullness index were both notably higher in Pacific cod juveniles, while walleye pollock juveniles were consuming greater numbers of comparatively smaller prey items. The dietary composition was also markedly different, primarily due to the increased number of large crustacean type prey items ingested by Pacific cod. Juvenile walleye pollock, in contrast, continued to consume large numbers of adult and copepodite stages of calanoid copepods.

In spite of the temporal and often spatial co-occurrence of age-0 walleye pollock and Pacific cod, the overall feeding patterns of larvae and juveniles were found to be significantly different in every season, both in terms of feeding success and dietary composition. These dietary differences suggest a form of prey partitioning and therefore indicate that dietary competition between early life stages of these two gadoid fishes is unlikely to occur, at least during cold conditions as experienced in 2008 in the southeastern Bering Sea.